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U.S. Forest Service Northern Conifer Experimental Forests: Historical Review and Examples of Silvicultural Research Applications

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U.S. FOREST SERVICE NORTHERN CONIFER EXPERIMENTAL FORESTS: HISTORICAL REVIEW AND EXAMPLES OF SILVICULTURAL RESEARCH APPLICATIONS

By

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By Kate Berven

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An Abstract of the Thesis Presented
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This study investigates U.S. Forest Service silvicultural research in the northern mixed-conifer forest of the Northeast. Chapter 1 is an overview of three closed experimental forests and is a cautionary tale regarding lost research opportunities. The Paul Smith, Finch-Pryun, and Gale River Experimental Forests (EFs) were established in the early to mid 1900s. Changing societal needs and research priorities led to redirected staffing and funding; all three were disestablished. Initial investments were lost and outcomes of the experiments not fully realized. This chapter highlights the importance of retaining and properly storing records.

The Penobscot EF is an exemplary illustration of replicated, long-term research. I used data from the silvicultural experiment in an evaluation of the Northeast Variant of the Forest Service's Forest Vegetation Simulator, a growth and yield model (Appendix B). In addition, chapters 2 and 3 examine seedlings and saplings in seven treatments on the Penobscot EF.

In Chapter 2, I examine the factors (treatment, density of regeneration, species, treatment interval, and site-specific factors) influencing recruitment into the sapling class. I found that shade-tolerant softwoods had a lower probability of recruiting into the sapling class than other species groups. Tolerant softwoods recruited at greatest densities in three-stage shelterwoods; other treatments had a slower, continuous rise in ingrowth. Species-specific trends should be investigated further.

Chapter 3 focuses on seedling herbivory. My analysis indicated that a seedling's probability of being browsed was a function of its height class and species. Tolerant hardwoods had the highest probability of being browsed, and tolerant softwoods the lowest. Among species of interest, red spruce and northern white-cedar had the highest species-specific probabilities of being browsed. Eastern hemlock and eastern white pine had relatively low browsing probability and severity, in contrast to findings from other regions. Because larger height classes had lower probabilities of browsing, release treatments may be beneficial.

Long-term data provide information regarding forest dynamics through time. Data from the Penobscot EF provide the opportunity to investigate trends over long temporal periods and across multiple silvicultural regimes. This knowledge may be useful when developing long-term goals and defining desired outcomes for silvicultural treatments.

DEDICATION

To my loving family,

Ryan, Nathan and Matthew

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

THE LOST RESEARCH OF EARLY NORTHEASTERN SPRUCE – FIR EXPERIMENTAL FORESTS: A TALE OF LOST OPPORTUNITIES

Introduction

Long-term research is critical to our understanding of forest dynamics. Observations made over decades or centuries provide valuable insight into the effects of natural and anthropogenic disturbances, and allow scientists and forest managers to determine which management regimes succeed and which ones fail in terms of desired objectives. Unfortunately, many long-term studies are closed before the full benefits of the research can be realized. When long-term projects end, it is often because values change and the research is considered less relevant (Innes 2004). Yet many old studies could inform contemporary forest management and policy, especially if combined with new research.

Long-term research in forest ecosystems requires steadfast dedication and more than one generation of scientists and forest managers. The U.S. Forest Service has been conducting research of this kind for over 100 years. Originally the Division of Forestry, the Forest Service was established in 1876 in response to the overwhelming need to conserve forested land and "sustain the health, diversity, and productivity of the Nation's forests and grasslands to meet the needs of present and future generations" (U.S. Forest Service 2010). The Forest Service works to maintain and improve the quality and production of more than 193 million acres of forests, wetlands and grasslands. The organization also serves state and private landowners, working to sustain public benefits from the nation's forests. Serving as a multifaceted organization, the Forest Service pursues many objectives from recreation management to research and development; the latter is conducted by six regional research stations in the United States.

The Northern Research Station (NRS) is the Forest Service's research and development program that extends across twenty states from the Midwest to the Northeast. It encompasses a diverse array of ecosystems and climatic zones, which create a broad scale for scientific inquiry (Rains 2006). The NRS, which includes the former North Central and Northeastern Forest Experiment Stations, is recognized for its extensive research and long-term projects; it maintains 22 of the Forest Service's 80 experimental forests and ranges (U.S. Forest Service 2009; Adams et al. 2008). Experimental forests provide opportunities for large-scale, long-term research. Studies conducted on experimental forests today have shifted from relatively localized and narrow themes to a broader range of issues relevant to global natural resource management problems (Lugo 2006).

The northern conifer forest extends from eastern Canada and Maine into the Adirondack Mountains of New York. These forests are characterized by a mixture of conifer species and northern hardwoods in varying proportions depending on factors including climate, aspect, elevation and site quality. Previously called "spruce-fir" forests, today these forests are described as northern mixed conifer forests or northern coniferous forests. They are typically dominated by red spruce (*Picea rubens*), black spruce (*Picea mariana*), white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*) with an element in varying amounts of northern hardwoods. Other species that are commonly present are eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*) and northern white-cedar (*Thuja occidentalis*). Historically, this forest type has been essential to the prosperity and economic well-being of the region. The lumber industry thrived due to favorable species composition and climatic conditions (Irland 1999); by the early 1900s the forests had been high-graded of the finest trees and were in a state of transition in terms of species composition and quality (Judd 1997).

When the NRS was founded in 1923, second-growth spruce – fir forests were increasingly dominated by poor quality hardwoods (Westveld 1938). Depletion of conifers due to high-grading, as well as the return of agricultural land to forests in the late 1800s and early 1900s, created urgency for research about conifer production (Westveld 1937). Because conifers were essential to the northeastern economy, as well as to the overall structure and characteristics of the forest type, early research conducted by the Forest Service in this region focused on methods to grow spruce and fir faster and eliminate hardwood competition. Prediction of forest yield was crucial to the future of the pulpwood industry and the long-term well-being of the forest (Westveld 1953). Experimental forests were the primary location of studies that supported this type of research.

Three spruce – fir experimental forests – the Gale River, Finch-Pruyn and Paul Smith Experimental Forests (EFs) – were established by the Station shortly after it was founded. Research and funding for these forests were motivated by the increasing demand for forest products. Indeed, from the 1920s to the 1940s, national assessments were gloomily predicting the exhaustion of the region's spruce-fir timber supply. As time progressed the relevance of the research faded and the experimental forests were closed, primarily due to lack of funding and the perception that scientific or practical values had shifted to other areas, though damage to research plots by natural disturbance was also a factor (Kenefic et al. in press).

Study Site

PAUL SMITH EXPERIMENTAL FOREST, NY

The Paul Smith EF, established in August of 1948 near Paul Smith's College in the Adirondack Mountains of New York (44 deg. 26'N, 74 deg. 14'W), is the most recent of the three early spruce – fir experimental forests. The forest was named to honor the famous guide, woodsman and land steward, Paul Smith. Because of its close proximity to the Finch-Pruyn, the two forests were jointly administered by the Forest Service's Adirondack Research Center with headquarters located in Paul Smiths, New York. The approximately 2,300-acre Paul Smith EF was administered under a 30-year cooperative agreement between Paul Smith's College and the Forest Service. In a 1954 radio broadcast for WNBZ in Saranac Lake, New York, Francis Rushmore, the lead scientist and research forester with the Forest Service, highlighted the objectives of the PSEF:

1. *The main objective of this cooperative program shall be the exploration, development and demonstration of economical methods of forest management adapted to the natural forests and climatic conditions of the Adirondacks and to the recreational and watershed values of the Adirondack region.*

2. *That this program is to be undertaken for the public benefits which will accrue, and that the interest of all people using and depending on the*

Adirondack forest region will be considered in the development of this program.

Selective logging altered the forest composition in New York, as it had in Maine and other areas in northern New England encompassing the eastern spruce-fir forests. A major difference was that the Adirondacks possessed a number of cutover old-growth hardwood stands (Rushmore 1957). Dendrochronology work at the Paul Smith EF in the 1950s indicated that it contained residual old growth; the oldest trees originated in the late 1600s, though repeated partial cutting and fire had since occurred (unpublished memorandum 1954). This facilitated the investigation of management problems not previously encountered in the region. The hardwood lumber industry in the area was confined to high quality sawlogs, but much of the forest was made up of low-quality, poorly formed trees (Curry and Rushmore 1955).

Experiments at Paul Smith EF involved various systems of destroying defective trees. Eliminating hardwoods was a chief goal for scientists and landowners alike. Girdling and application of chemicals were the primary methods used. Sodium arsenite and ammonium sulfamate were applied during different seasons to evaluate dieback and death (Curry and Rushmore 1955). Frilling was also used to kill unwanted trees; this process involved bark removal and application of sodium arsenite to the cambium layer of the tree (Rushmore 1956). Though researchers at the time often turned to chemical-based silviculture, many other studies were conducted and formed the leading edge of eastern spruce-fir management. Understanding the growing public concern surrounding the quality of the forest and the future of the lumber industry, Forest Service researchers at Paul Smith EF conducted a number of studies of stand improvement and regeneration methods.

Fifty-five 40-acre compartments were established in a large-scale experiment to study a variety of silvicultural methods and harvest intensities (Figure 1.1). Methods included all-aged (uneven-aged) treatments with 10-, 20- and 30-year cutting cycles, as well as even-aged treatments such as shelterwood and clearcutting. Timber stand improvement methods, including thinning and crop tree release, were also investigated. Emphasis was put on control of competing hardwoods through cultural treatment (unpublished memorandum 1953). Rushmore (1954) said that forests should be tended like a vegetable garden. "We know that weeds must be removed from our gardens or our crops will be choked out; the forester must frequently remove worthless trees or his better ones will not grow as well as they can. And, we must harvest our garden crops when they ripen, or they will become worthless; the forester must also harvest his trees as they reach maturity or they will begin to rot and will eventually become worthless." These stand improvement techniques, though commonly used in today's forests, were new concepts for forest managers of the time.

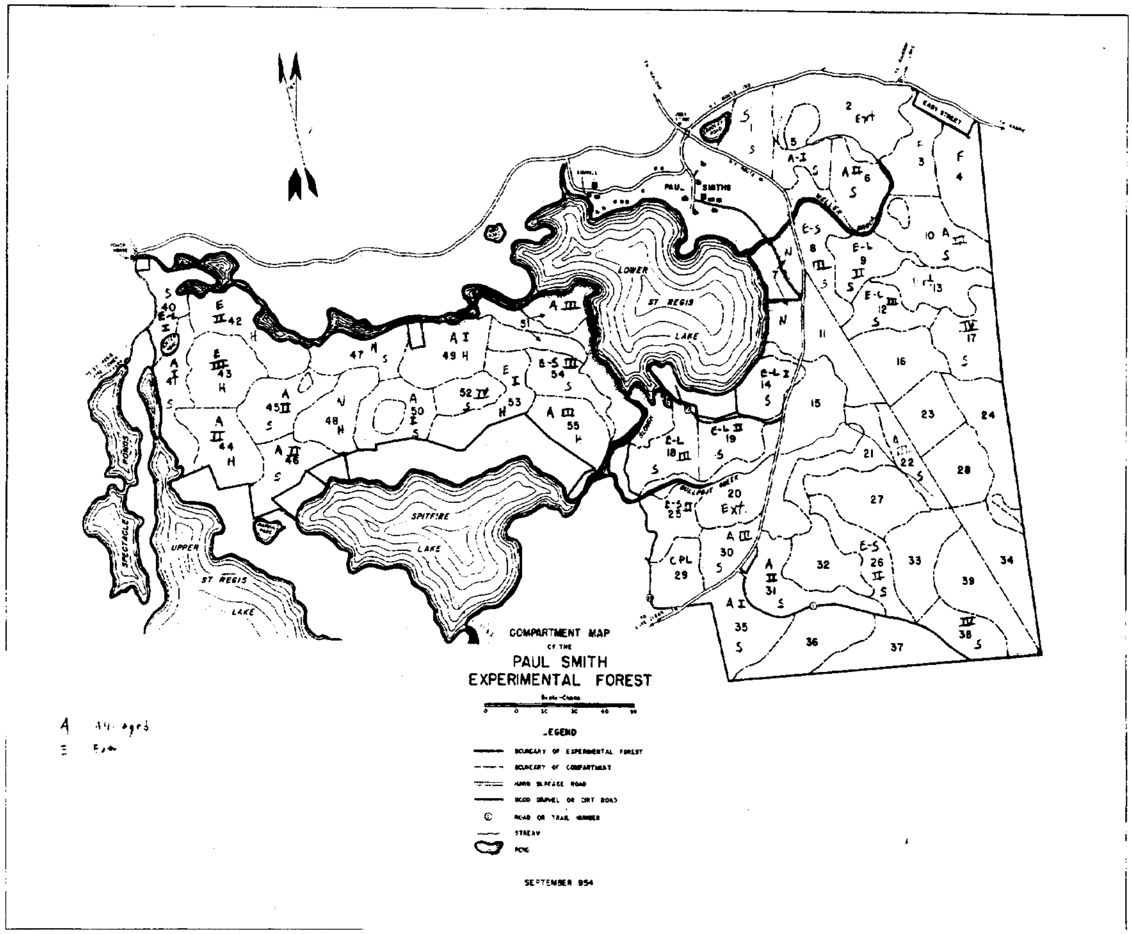

Figure 1.1. Compartment map of the Paul Smith Experimental Forest (1954). Map courtesy of the U.S. Forest Service and Paul Smith's College.

<u>Compartments</u>

Three of the Paul Smith EF compartments will be discussed here, and are typical of the research on the experimental forest in the 1940s and 1950s. The cutting practice level (CPL) study (compartment 29) on the Paul Smith EF was initiated in 1950 in order to demonstrate a range of silvicultural intensities for the spruce – yellow birch (*Betula alleghaniensis*) forest type, and would serve as a guide to achieving the most productivity from the forest (unpublished working plan 1949, unpublished establishment report 1951).

These demonstrations were common on experimental forests in the 1940s. The cutting levels, which included "high-order," "good," "fair," and "poor-order," were designed to demonstrate forest responses and guide future management decisions. The "high-order" and "good" treatments, which were forms of selection cutting, were intended to provide long-term growth on high-quality trees. These two treatments were intended to build spruce growing stock by removing only poor quality, competing trees. "High-order" treatments were distinguished from "good" by having higher guiding diameter limits for spruce and fir and a shorter cutting cycle (5 to 10 years versus 15 to 20 years). The "fair" treatment was a form of diameter-limit cutting with tending in which all merchantable trees were removed except for spruce smaller than 12" diameter at breast height (dbh). Harvest intervals in the "fair" treatments were 25 to 35 years. The "poor-order" treatment was a commercial clearcut, which left unmerchantable and low-quality timber; the harvest interval was greater than 50 years. Today, remnants of the study are still visible, and large-diameter red spruce and yellow birch trees can be found throughout the compartment where the "high-order" treatment was applied (Figure 1.2) (L. Kenefic, personal communication).

Figure 1.2. Compartment 29, high-order treatment (2010). Photo courtesy of U.S. Forest Service.

Compartment 19, a stand improvement study, was composed of two sub-compartments. The first was a spruce – yellow birch stand containing little softwood reproduction; the second was a mixed conifer – paper birch (*Betula papyrifera*) stand containing a large component of white pine and abundant softwood regeneration. Because of abundant softwood advance reproduction, both sub-compartments were treated with "good" silvicultural treatments, using a uniform shelterwood. The first cut left approximately 50 ft^2 per acre of softwood basal area. Overstory removal was to be conducted 10 years later with poisoning of competing trees ≥ 6" in diameter at breast height (unpublished memorandum 1954). Stand improvement work was conducted in which overstory hardwoods were removed where ample regeneration was present. There was also a small area in the southwest portion of compartment 19 designated for planting of red spruce by Paul Smith's College as a part of a forestry class. Although a future overstory removal and subsequent thinnings were planned, there is no paperwork to confirm that any harvesting was conducted after the initial regeneration cut and stand improvement treatments. Today, large residuals of white pine, red spruce and yellow birch are scattered throughout the compartment (Figure 1.3).

Figure 1.3. Compartment 19: residual trees from the Paul Smith EF (2010). Photo courtesy of U.S. Forest Service.

Compartment 35 was also subdivided into two forest types; spruce – yellow birch and spruce – fir. This compartment was assigned high-order selection treatments with 10-year cutting cycles. These harvests focused on removing cull or poorly formed trees, building to a growing stock of 2,000 ft^3 ac^{-1} of spruce and fir at the end of the cycle. Poor quality, merchantable sawlogs were cut while cull hardwoods above 5" dbh were poisoned or girdled. Results from this study after 10 years showed that objectives had not been met for either forest type, falling below the volume goal. Hardwoods were reduced in numbers, but volume in the spruce – fir type totaled 1,614 cubic feet, while the spruce – yellow birch type contained only 793 cubic feet at the end of the 10 year cycle. Plans for future treatments in this compartment included weeding and timber stand improvement to reduce hardwood competition, but it was concluded that cultural operations would be too costly given market conditions.

FINCH-PRUYN EXPERIMENTAL FOREST, NY

The Finch-Pruyn EF, established by the Forest Service in 1934 near Newcomb, New York (44 deg. 00'N, 74 deg. 13'W), was the second of the spruce – fir experimental forests to open. Comprising approximately 623 acres in the Adirondack Mountains, it was deeded to Cornell University by Finch, Pruyn and Company, Inc. in 1934 for studies in spruce and northern hardwood management; Cornell subsequently signed a cooperative agreement with the Forest Service. We have very little information about research done on the Finch-Pruyn EF, though a 1942 working plan describes girdling plots in the red spruce – yellow birch and red spruce – sugar maple (*Acer saccharum*) – American beech (*Fagus grandifolia*) forest types. Girdling was conducted on hardwoods to release spruce in the understory. There are no field notes or measurement records of this work in the Forest Service archives, though some publications from this time appear to use Finch-Pruyn EF data, e.g. a paper by Recknagel et al. (1933) which describes a series of plots on the Finch-Pruyn EF; these were installed to determine the effects of different cutting methods on residual stand composition and tree growth rates.

Both the Paul Smith and Finch-Pruyn EFs remained open until 1961 when the Adirondack Research Center closed. After closing, papers documenting the work, including study plans and data sheets, were left with Paul Smith's College and the Paul Smith EF was integrated into the College forest. Over the years, the files were moved around and eventually forgotten. It wasn't until a visit to the school during the summer of 2009 that research materials were found in the basement of a dormitory. These files have subsequently been made available for on-site review and will soon be digitized by the Forest Service and made available electronically. Preliminary site visits suggest that while some of the compartments have been harvested, others remain intact and may yield worthwhile remeasurement data.

GALE RIVER EXPERIMENTAL FOREST, NH

Research at the 1,623-acre Gale River EF, located near Bethlehem, New Hampshire (44 deg. 51'N, 68 deg. 37'W) in the White Mountains, began in 1927. It was the first experimental forest in the region. Marinus Westveld (Figure 1.4), a Senior Silviculturist and the pioneer of spruce – fir silviculture, set up and conducted most of the research on the Gale River EF. It was because of a growing pulpwood industry and the continual reduction in pulpwood-producing land that he began his research in spruce-fir silviculture, to ensure and maintain a healthy component of softwoods in the forest where competing hardwoods were present (Westveld 1937). Because many acres of forestland in the early twentieth century were on former agricultural fields, hardwood exclusion was also a priority to ensure the continual production of spruce-fir forests. There was particular interest in partial cutting experiments, including the removal of only sawtimber-sized trees (Kenefic et al. in press; Kraemer 1937). Westveld's innovative work in modeling growth and yield in these forest types, as well as his "selective" cutting practices, led to the widespread use of uneven-aged management practices (Kenefic et al. in press).

Figure 1.4. Marinus Westveld (left), the grandfather of spruce-fir silviculture, at the Gale River Experimental Forest (note peeled spruce). Photo courtesy of the U.S. Forest Service.

The Great New England Hurricane of 1938 destroyed the majority of the studies at the Gale River EF as well as research plots in Ripton, Vermont and Cherry Mountain and Waterville, New Hampshire (Figure 1.5). A weeding study initiated in the fall of 1933 was the only remnant of the experiments conducted, with the exception of several small plantations. Overstory removal during the course of the weeding experiment left young crop trees that were not large enough to be damaged by the hurricane seven years later (Westveld 1937). The purpose of the study was to determine the effectiveness of different methods of killing competing hardwoods, and to document the growth dynamics of released white spruce (unpublished memorandum 1933).

Figure 1.5. The Great New England Hurricane of 1938 destroyed much of the Gale River EF and surrounding areas. Photo courtesy of the U.S. Forest Service and Forest History Society.

Ten plots were established in the weeding study to investigate different methods of killing competing and overstory hardwoods including cherry (*Prunus spp.*), red maple (*Acer rubrum*), American beech and birch (*Betula spp.*) (unpublished memorandum 1948). The treatments included girdling, cutting and applying a sodium arsenite solution. Cope tools were used in blocks one through eight to deliver the poison in varying levels including one jab, numerous jabs and 100% treatment around the circumference of the tree. In block nine, axes were used for overstory removal; chainsaws and clippers were used in block ten (unpublished memorandum 1936). Six additional 1/10-acre plots were established to ascertain the influence of season on girdling response; these were too severely damaged by the hurricane to provide useful information and were abandoned.

Eventually, the research measurements that had continued after the hurricane diminished. By 1941, the personnel stationed on the Gale River EF withdrew and the EF was placed in an inactive status. In 1950, another hurricane swept through the area, causing more damage. Salvage was conducted, but Station management's wish to relinquish the property increased because most of the research had been destroyed. Westveld had continued to take measurements for over 15 years after the EF became inactive and believed that the forest had value for research (unpublished U.S. Forest Service memorandum 1956). However, the Gale River EF was officially closed in 1958 and transferred to the White Mountain National Forest.

A small number of the Gale River EF research files were sent to the field office in Maine and forgotten until their rediscovery in the attic of a now-demolished building in 2008. The bulk of the files had been sent to the Federal Records Center (FRC) (unpublished memorandum 1958). Such files may have been destroyed per a Forest Service-approved disposition schedule, or transferred to the National Archives and Records Administration (NARA). The paperwork needed to recall the records has been lost and recent efforts to locate the Gale River EF files through the FRC and NARA have been unsuccessful.

Believing there was potential to re-establish the weeding study, I visited what was once the Gale River EF in 2009. Arriving there to find mortality from a 1980s windstorm, thinning by the National Forest and no field notes or measurement data from the research conducted decades prior, I determined that there was no possibility for re-opening the study. Nevertheless, I monumented nine of the ten blocks established by Westveld in 1933 and took a series of measurements to determine species composition and stocking (the tenth block had been converted to a wildlife clearing by the National Forest). Average basal area was determined for each block (Figure 1.6). Today, approximately 19% of the total basal area per acre and 24 trees per acre in the former study area are white spruce. Regeneration from the white spruce crop trees is also present; these are the remnants of Westveld's work at the Gale River EF.

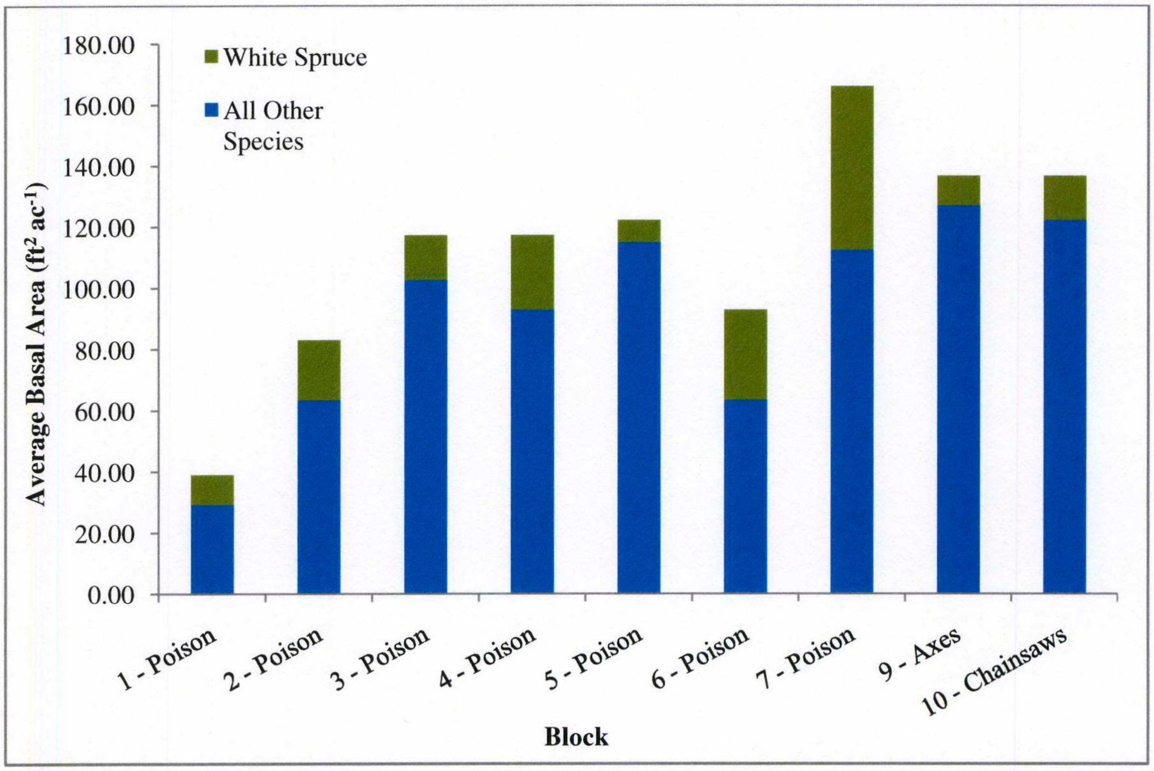

Figure 1.6. Average basal area (ft^2 ac^{-1}) by block in the former Gale River EF wedding study (2009). Blocks represent different weeding methods applied by Marinus Westveld in 1933 to remove unwanted hardwoods for release of planted white spruce.

PENOBSCOT EXPERIMENTAL FOREST, ME

Shortly before the Gale River EF was transferred to the White Mountain National Forest, another spruce – fir experimental forest was established in east-central Maine. The Penobscot EF located in the towns of Bradley and Eddington, Maine encompasses approximately 4,000 acres. Research there was profoundly inspired by Westveld's ideas advocating uneven-aged management in spruce – fir forests (unpublished U.S. Forest Service problem analysis 1950), though a full range of silvicultural systems were included in the experiment. Replicated treatments were initiated at the Penobscot EF between 1952 and 1957 (Sendak et al. 2003) and have since been a premier example of collaborative, sustained forestry research (Brissette et al. 2006). Full replication and repeated application of treatments in long-term silviculture studies is uncommon and makes the Penobscot EF a unique and highly valued research site. Results from the research are continually emerging, providing valuable insight to practitioners and policy makers alike (Kenefic et al. 2006). Furthermore, the diversity of stands and associated variability in composition and structure provide opportunities to overlay new research projects (Nowak et al. 1997). Though the Station considered transferring the Forest Service staff working at the Penobscot EF to another location in the 1980s, local support for the research prevented this action (Kenefic et al. in press). The Penobscot EF is the product of decades of dedication shown by the foresters and scientists that saw the value of continuing the study.

Summary

On all three of the early spruce – fir experimental forests, treatments were discontinued and the research areas subject to natural disturbances or undocumented management. However, they do provide valuable insight to the early silvicultural research conducted in eastern spruce – fir forests. Failure to fully preserve historical documents hampered our ability to capture the relevance of the work through re-measurement and analysis. Without initial measurements, it is impossible to relate historical treatments to forest condition today. In the past 80 years, ownerships have changed, people have come and gone and the landscape has changed based on the needs of a growing population. The potential value of these studies, had they been maintained, is unknown. At the very least, a glimpse into the past can provide historical reference and offer insight about our predecessors. The 60 years of research at the Penobscot EF are invaluable, but represent only a portion of the Forest Service's eastern spruce – fir research over the past century. The closed experimental forests and the publications from the studies there (Appendix A) serve as a reminder of the legacies left by the pioneers of early silviculture in eastern spruce – fir forests and as a cautionary tale of how years of research can be lost if records are not preserved.

CHAPTER 2

SAPLING RECRUITMENT ON THE PENOBSCOT EXPERIMENTAL FOREST: HOW LONG-TERM DATA CAN PROVIDE INFORMATION ABOUT STAND DYNAMICS FOLLOWING DISTURBANCE

Introduction

In managed, naturally regenerated forests, understanding regeneration dynamics and recruitment into the sapling class is important for determining future stand composition and growth potential. Thus, the second chapter of the thesis focuses on regeneration and recruitment in the U.S. Forest Service experiment on the Penobscot Experimental Forest (PEF) in Maine. The PEF is an excellent source of data due to the long-term nature of the experiment and the range of silvicultural treatments applied. Due to the history of the region and the current predominance of partial-cutting practices (Maine Forest Service 2008), newly regenerated cohorts often develop under multi-aged, stratified canopies before being recruited or succumbing to mortality (Ray et al. 2008). Recruitment failures can alter stand and forest dynamics and may have dramatic effects on tree and plant communities (Ribbens et al. 1996).

Much of our knowledge of stand dynamics is based on Oliver (1981), who identified four primary stages of stand development: stand initiation, stem exclusion, understory reinitiation, and old growth. Regeneration occurs in all stages, except stem exclusion, during which competition for sunlight prevents establishment and creates high mortality in suppressed individuals. Recruitment can occur in all stages, however. Controlling overstory stocking may facilitate the establishment and release of new trees

(Smith 1962). However, there has been little research in the Acadian Forest on regeneration and recruitment dynamics, and the influence of site, stand characteristics, and silvicultural practices on those dynamics.

Recently, Olson (2009) discussed regeneration dynamics with regard to disturbance on the Forest Service's long-term silviculture experiment on the PEF. He found that mixed hardwood species including paper birch (*Betula papyrifera*), grey birch (*Betula populifolia*), American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), trembling aspen (*Populus tremuloides*) and bigtooth aspen (*Populus grandidentata*), have increased in importance over the past five decades due to repeated cuttings. Balsam fir (*Abies balsamea*), a prolific species which produces high volumes of seed (Seymour 1992) and increases in height faster than red spruce (*Picea rubens*) (Westveld 1925, Moores et al. 2007) has remained dominant within the forest as other conifer species have declined, despite fir's vulnerability to pests and decay, and stricter site requirements (Seymour 1992).

Because spruce has many valuable characteristics including longevity, greater resistance to spruce budworm (*Choristoneura occidentalis*), ability to compartmentalize decay (Seymour 1992), and is more valuable (Sendak et al. 2003), it is usually the species for which regeneration and recruitment efforts are focused in the northern conifer forest. From the early 20th century, silvicultural goals in the northern mixed-conifer forests have focused on increasing spruce, while decreasing hardwoods (Westveld 1928, 1953). Natural regeneration is prolific in the region and occurs under partial shade to full sunlight (Sendak 2003). Spruce seedlings may remain in the understory for long periods of time before recruiting into larger size classes (Weaver 2007). Because of the slow-growing nature of these species, advance regeneration is necessary to outcompete faster growing, less shade-tolerant species when canopy gaps occur (Seymour 1992). Without advance regeneration, regenerated stands often become dominated by shade-intolerant or sprout-origin hardwoods (Hart 1963).

Recruitment to the sapling class (≥ 1.3 cm in diameter at breast height [dbh]) in the past 30 years in the silviculture experiment on the PEF has been measured and recorded; these data provide details about the species composition and density of stems entering the sapling class. Investigation of regeneration and recruitment trends can provide insight to stand structural and compositional changes over time, and provide site-specific information about factors influencing recruitment.

Tolerant softwoods are the defining species group of the northern mixed-conifer forest. In stands such as these, where rainfall is abundant, regeneration failures are not common (Seymour 1992), but sapling recruitment is highly variable. Because managing forests to promote this group is often the goal in this forest type, considering the trends of tolerant softwoods as compared with other shade-tolerance groups is of interest.

The purpose of this study was to investigate recruitment dynamics over long temporal scales using the PEF's dataset; recruitment has been measured and recorded since the mid-1970s. Understanding the dynamics and processes occurring across species and treatments over long temporal scales provides insight into how disturbances, as well as other factors, influence species' ability to enter larger size classes. Specific objectives of this study were:

(1) to predict the probability of recruitment occurring given the amount of regeneration present, silvicultural treatment, and time since treatment;

(2) given the occurrence of recruitment, assess the amount by shade tolerance group, silvicultural treatment, and time since treatment;

(3) assess the influence of plot-level factors such as soils, stand density and distance from stand edge on recruitment amount.

Methods

STUDY SITE

The 1680-ha PEF is located in the towns of Bradley and Eddington, Maine in Penobscot County (Figure 2.1). The PEF is part of the northern mixed-conifer forest, which extends from southeastern Canada and Maine to the Adirondack Mountains of New York, comprising an ecotone between boreal and eastern broadleaf forests (Sendak et al. 2003). The forests are characterized by a mixture of conifer species and northern hardwoods in varying amounts depending on a number of different factors including climate, aspect, elevation, and site quality. The Acadian Forest (Rowe 1972) of central Maine and adjacent Canada is typically dominated by red spruce, white spruce, eastern hemlock and balsam fir with varying amounts of northern hardwoods including trembling aspen, bigtooth aspen, paper birch, yellow birch (*Betula alleghanensis*), American beech, red and sugar maple, and cherry (*Prunus spp.*). Other species that are commonly present are eastern white pine (*Pinus strobus*) and northern white-cedar (*Thuja occidentalis*).

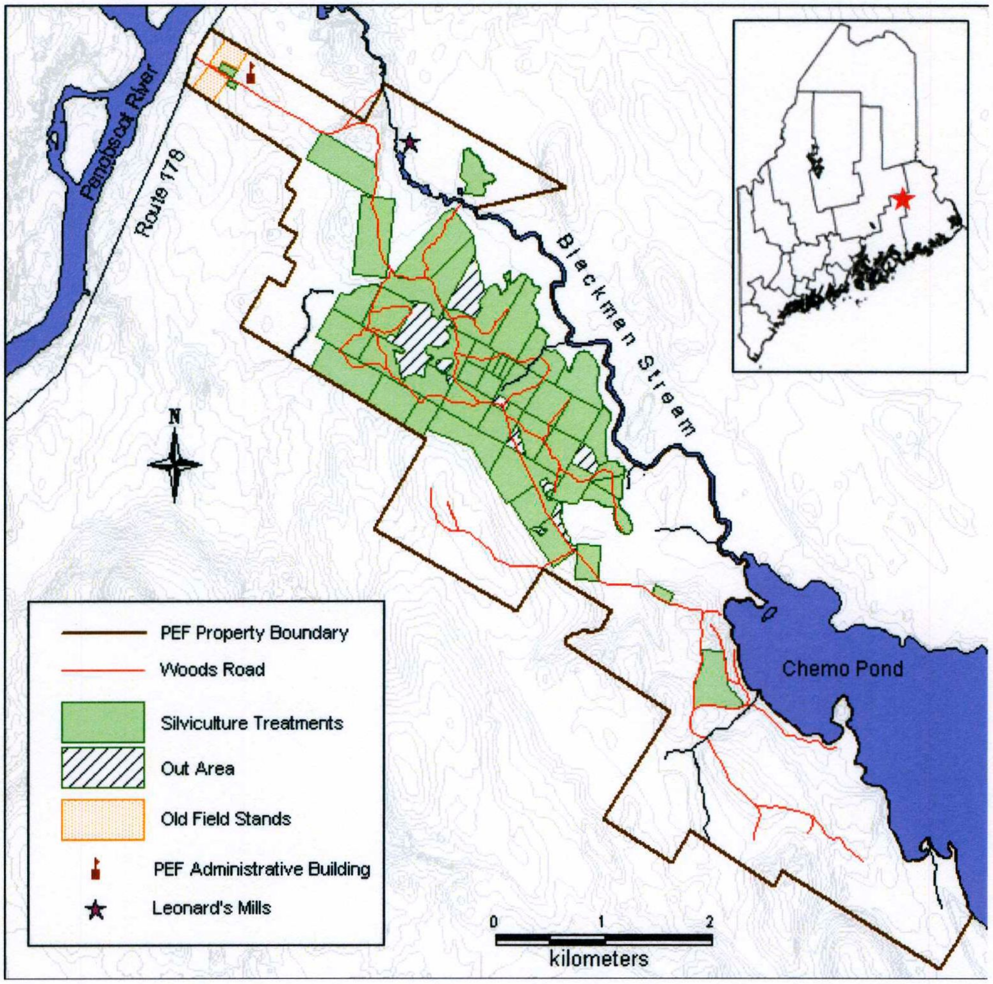

Figure 2.1. Map of the Penobscot Experimental Forest (Bryce 2009).

Soils on the PEF are Wisconsin glacial till derived from fine-grained sedimentary rock and tend to be thin, shallow, wet spruce-fir flats. Glacial till ridges are well-drained stony and Plaisted loams and moderately well-drained sandy and Howland loams. Flat till areas located between ridges are comprised of poorly and very poorly drained silt, Monarda and Burnham loams (Safford et al. 1969). Climate in central Maine is cool and humid. Mean annual temperature is 6.6° C and average precipitation is 106 cm. The growing season is approximately 160 days.

Land use history of the area prior to establishment of the PEF in 1950 is not well documented. The forest appeared to be irregular in age and size structure when the land was purchased. Descriptions of the area that would become the PEF were recorded on maps in the 1920s and 1940s (on file with the U.S. Forest Service). The study area was described in 1929 as "mixed softwood second growth" with pole-size spruce and fir, hemlock up to sawtimber size, scattered hardwoods and good spruce and fir regeneration and as "operable spruce-fir-hemlock" in 1949. These conditions were most likely a result of natural stand development and a long history of periodic partial cutting (Sendak et al. 2003; Kenefic et al. 2006). Large-scale, stand-replacing natural disturbances are uncommon in the Acadian region and have a return interval of 250-800 years (Lorimer 1977), although small-scale, gap-forming disturbances and periodic spruce budworm outbreaks (most recently in the 1970s and 1980s) are common (Seymour et al. 2002).

The PEF is unique because it is a long-term research site containing twice-replicated silvicultural treatments on 170 ha, established by the Forest Service between 1952 and 1957 (Sendak et al. 2003). Treatments included in this large-scale "compartment" study include: the selection system on 5-, 10-, and 20-year cutting cycles, commercial clearcutting (also called unregulated harvesting), fixed and modified (also called flexible) diameter-limit cutting, uniform shelterwood with two- and three-stage overstory removals (the three-stage shelterwood was later subdivided into four stands, two of which were precommercially thinned) and an unmanaged reference. Treatments were staggered in time so that treatment intervals coincided with management objectives and not dates (Figure 2.2). Changes over time in species composition and basal area of trees ≥ 1.3 cm in the treatments used in the present study can be seen in Figures 2.3 and 2.4.

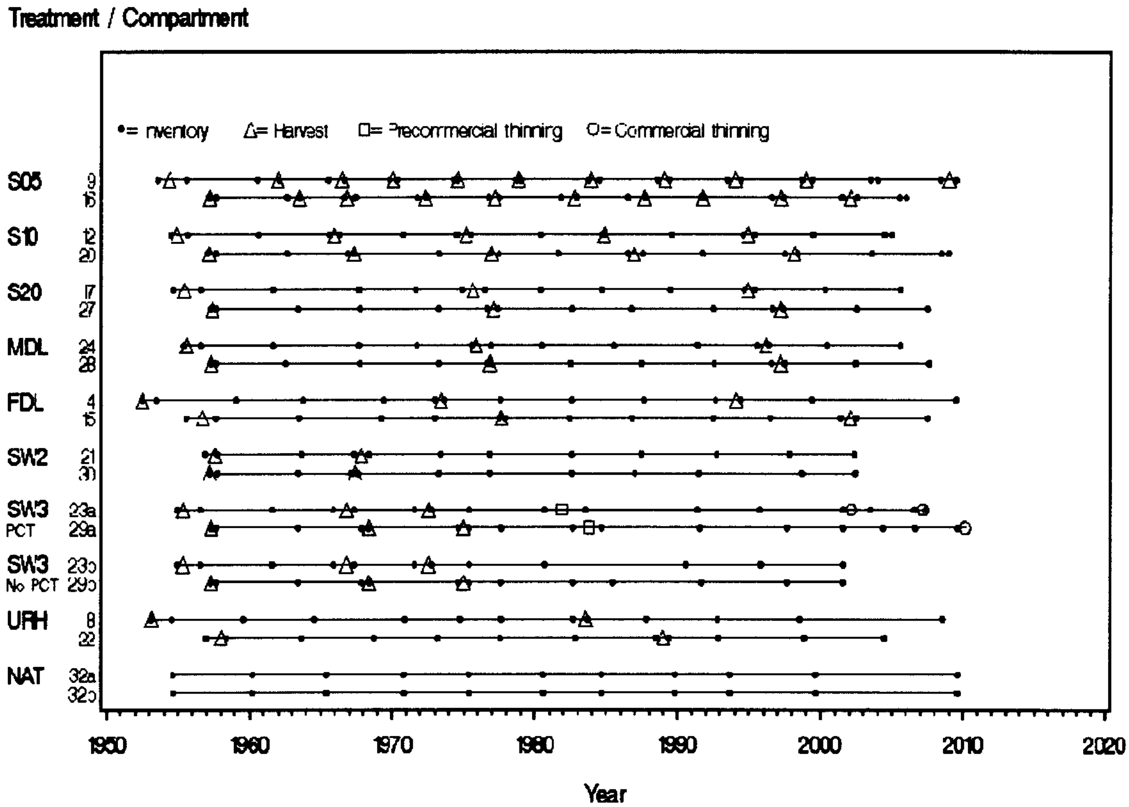

Figure 2.2. Treatment history on the PEF including inventories, harvests, pre-commercial and commercial thinning, courtesy of John Brissette, U.S. Forest Service.

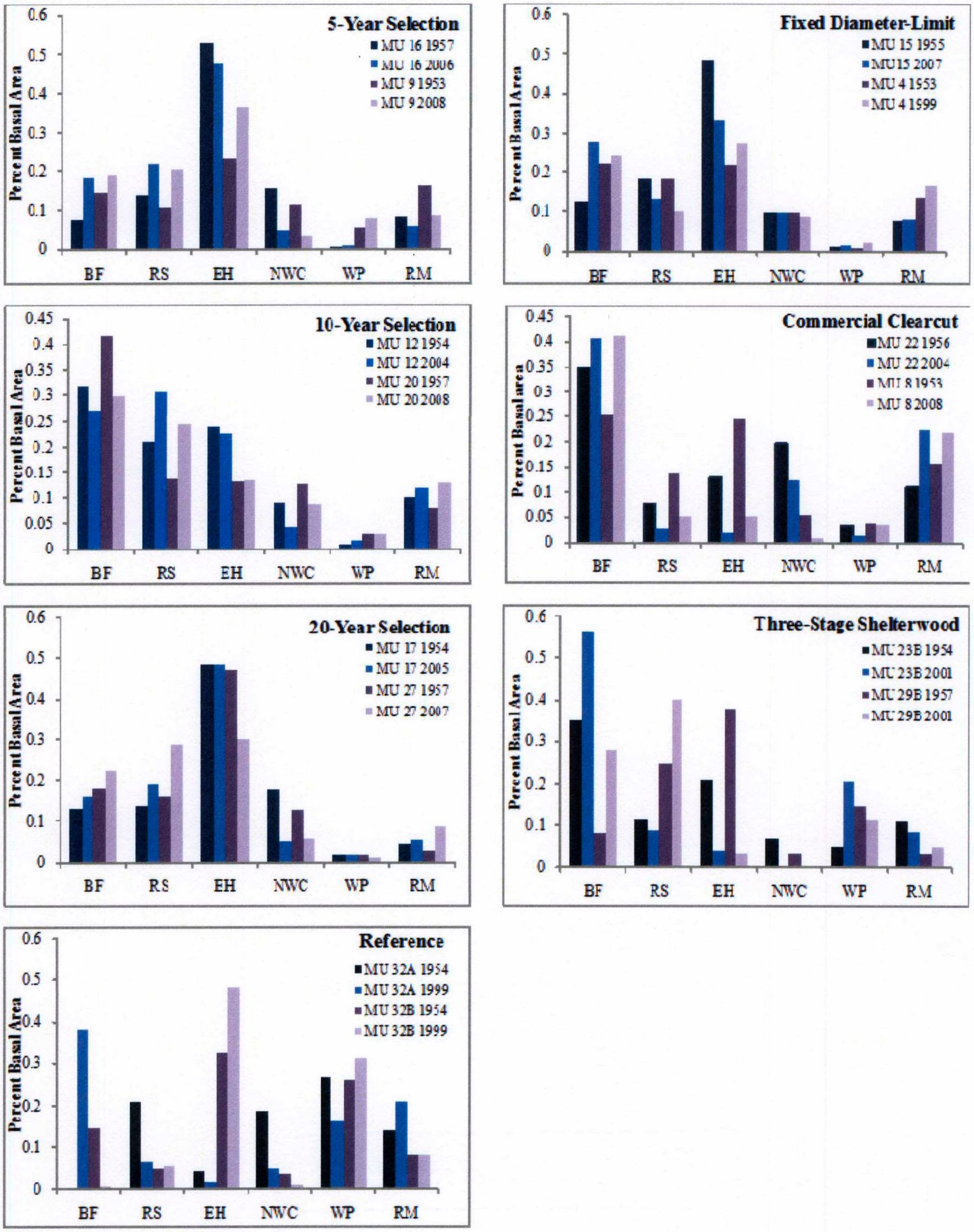

Figure 2.3. Proportion of basal area by species for the first and last inventory of each compartment (management unit [MU]). Species codes used in this graph are as follows: balsam fir (BF), red spruce (RS), eastern hemlock (EH), northern white-cedar (NWC), white pine (WP), and red maple (RM). Other species present is minor amounts are not shown.

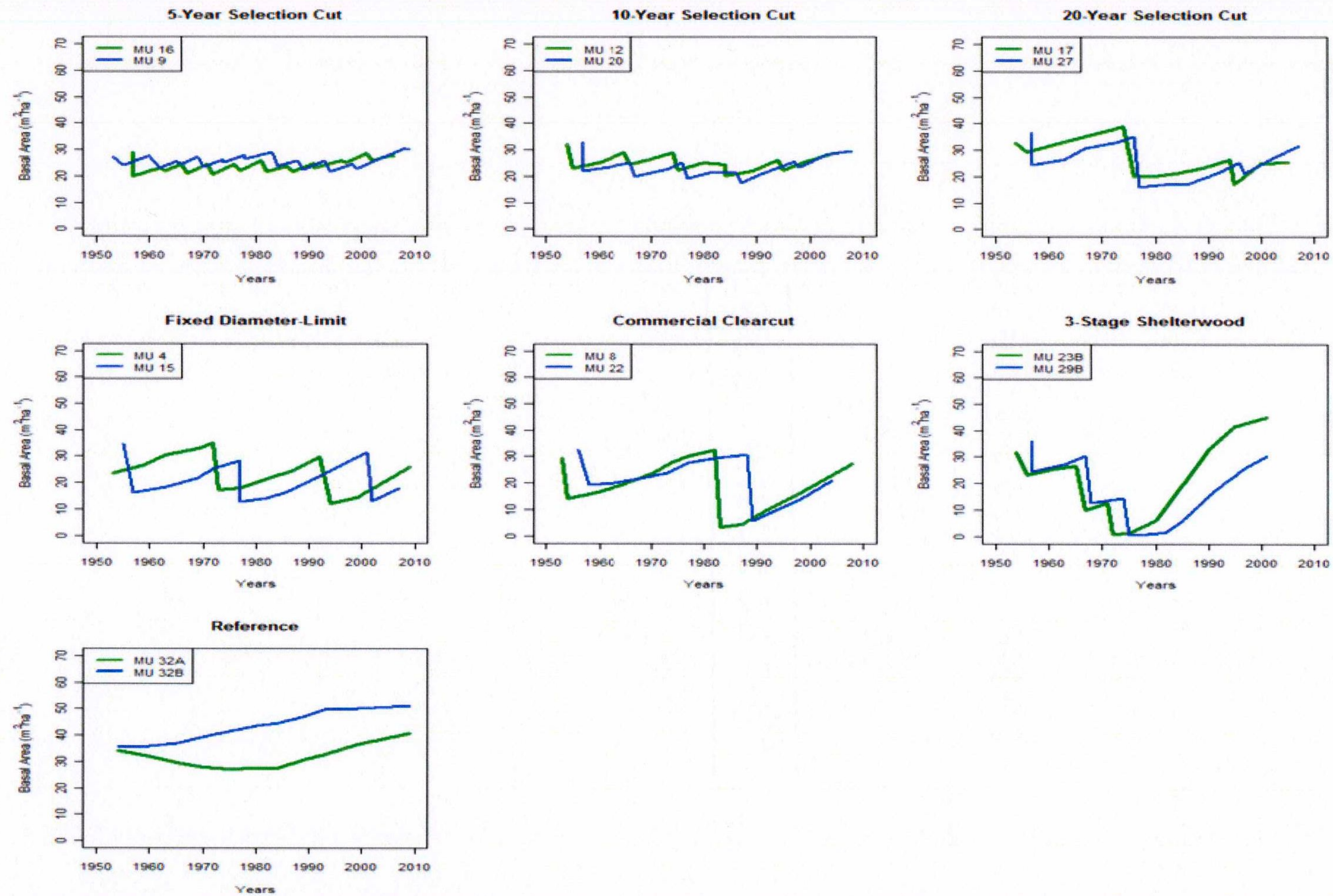

Figure 2.4. Graphs of total basal area (BA; $m^2\,ha^{-1}$) since treatment establishment on the Penobscot Experimental Forest. Data provided by the U.S. Forest Service.

Though the land for the PEF was bought by nine timberland owners in Maine and leased to the Forest Service for a commodity-production experiment, the study evolved to address the effects of silviculture and exploitive harvesting on stand dynamics and other forest concerns including productivity, resiliency and biological diversity (Sendak et al. 2003). When the experiment began, only basic mensurational data were collected, however over the past 60 years, research expanded to include leaf area and growth efficiency as well as course woody debris and regeneration, among other topics (for example, Kenefic and Seymour 1999; Seymour and Kenefic 2002; Weaver et al. 2009; Brissette et al. 2003; Kenefic et al. in press). Response variables measured in the long-term silvicultural study on the PEF currently include regeneration, species composition, tree and stand growth, productivity and quality (unpublished study plan, 2008).

The seven treatments measured for the current study are: no management (reference, UC), three-stage shelterwood (3SW), fixed diameter-limit cutting (FDL), commercial clearcutting (CC), and selection cutting on 5-, 10- and 20- year cutting cycles (S05, S10, and S20 respectively). All replicates of the treatments were measured, for a total of 14 compartments (stands) (Table 3.1). Diameter limits and BDq (basal area, maximum diameter and q factor [Meyer 1952]) thresholds for the uneven-aged silviculture systems are found in Table 3.2. Compartments range in size from 2 to 17 ha. There are 8 to 21 nested 0.08-, 0.002-, and 0.008-ha Continuous Forest Inventory (CFI) plots in each compartment; these are inventoried every 5 or 10 years and before and after each treatment and provide a 15% sample of each stand. Prior to year 2000, saplings ≥ 1.3 cm DBH were measured on the nested 0.02-ha plot (Figure 2.5); beginning in year 2000 saplings were measured on nested 0.008-ha plots (Figure 2.6). Inventory data include species and DBH for trees > 1.3 cm. Regeneration inventories began in the mid-1960s, and include counts of seedlings by species and height classes (Table 2.3). There are three to four milacre regeneration plots around the perimeter of each 0.02-ha plot (Figure 3.5).

Table 2.1. Silvicultural treatments, compartments and treatment dates used for recruitment analysis on the Penobscot Experimental Forest in Bradley and Eddington, Maine.

Compartment	Treatment	Treatment Abbreviation	Treatment Description	Size (ha)	Treatment Dates
32A	Unmanaged Reference	UC	No management conducted after compartments were established. There had been unspecified partial cutting prior to 1900.	5.2	-
32B				2.2	
8	Commercial Clearcut	CC	Removal of all merchantable stems.	17.5	1953, 1983
22				13.7	1955, 1988
23B	3-Stage Shelterwood	3SW	Establishment cut followed by two overstory removal cuts.	5.0	1955, 1966, 1972
29B				3.0	1957, 1968, 1974
15	Fixed Diameter-Limit	FDL	Trees removed above specified diameters on variable cutting cycle. Harvests scheduled when volume achieves 147 m^3 per ha.	10.3	1956, 1971, 2001
4				10.1	1952, 1973, 1994
9	5-Year Selection Cutting	S05	Single-tree and small-group selection on a 5-year cutting cycle with periodic mechanical (brushsaw) release of selected saplings.	11.0	1954, 1961, 1966, 1970, 1974, 1978, 1983, 1989, 1993, 1998, 2003
16				6.6	1957, 1963, 1966, 1972, 1977, 1982, 1987, 1991, 1997, 2001, 2006
12	10-Year Selection Cutting	S10	Single-tree and small-group selection on a 10-year cutting cycle.	12.6	1954, 1965, 1975, 1984, 1994
20				8.6	1957, 1967, 1976, 1986, 1998
17	20-Year Selection Cutting	S20	Single-tree and small-group selection on a 20-year cutting cycle.	10.7	1955, 1975, 1994
27				8.2	1957, 1977, 1997

Table 2.2. Specific threshold levels for four treatments on the PEF from four study plans since experiment establishment. Note: q factors are expressed for 2.54-cm diameter classes.

Treatment	Date of Study Plan[1]	Threshold Descriptions
Fixed Diameter-Limit	1953	Thresholds are 16.5 cm for balsam fir, 24.1 cm for spruce and hemlock, 26.7 for white pine, 19.1 cm for paper birch, and 16.5 cm for other hardwoods.
	1962	Thresholds are 16.5 cm for balsam fir, 24.1 cm for spruce and hemlock, 29.2 cm for white pine, 19.1 cm for cedar, 21.6 cm for paper birch, and 16.5 cm for other hardwoods.
	1974	Thresholds are 11.4 cm for balsam fir, 24.1 cm for spruce and hemlock, 26.7 cm for white pine, 19.1 cm for cedar, 19.1 cm for paper birch, and 11.4 cm for other hardwoods.
	2008	Thresholds are 14.0 cm for balsam fir, 24.1 cm for spruce and hemlock, 26.7 cm for white pine, 19.1 cm for cedar, 19.1 cm for paper birch, and 14.0 cm for other hardwoods.
5-Year Selection Cutting	1953	Structural goals are to retain 32.1-36.7 m^2/ha (trees > 1.3 cm), residual max diameter of 40.6 cm for pulpwood and 61 cm for multiple products, and q = 1.45 for pulpwood and 1.4 for multiple products.
	1962	Structural goals are to retain 27.5 m^2/ha (trees > 1.3 cm), residual max diameter of 40.6 cm for pulpwood and 61 cm for multiple products, and q = 1.4 for pulp and 1.3 for multiple products.
	1974	Structural goals are to retain 26.4 m^2/ha (trees > 1.3 cm), residual max diameter of 50.8 cm, and q = 1.4.
	2008	Structural goal is to retain 24.1 m^2/ha (trees > 11.4 cm). Residual max diameter and q factor vary by species group.
10-Year Selection Cutting	1953	Structural goals are to retain 32.1 - 36.7 m^2/ha, residual max diameter of 40.6 cm for pulp and 61 cm for multiple product, and q = 1.45 for pulp and 1.4 for multiple product.
	1962	Structural goals are to retain 24.1 m^2/ha (trees > 1.3 cm),, residual max diameter of 40.6 cm for pulp and 61 cm for multiple product, and q = 1.4 for pulp and 1.3 for multiple products.
	1974	Structural goals are to retain 23.0 m^2/ha (trees > 1.3 cm), residual max diameter of 50.8 cm, and q = 1.4.
	2008	Structural goal is to retain 20.7 m^2/ha (trees > 11.4 cm). Residual max diameter and q factor vary by species group.
20-Year Selection Cutting	1953	Structural goals are to retain 25.3 - 29.8 m^2/ha, residual max diameter of 40.6 cm for pulp and 61 cm for multiple product, and q = 1.45 for pulp and 1.4 for multiple product.
	1962	Structural goals are to retain 18.4 m^2/ha (trees > 1.3 cm),, residual max diameter of 40.6 cm for pulp and 61 cm for multiple product, and q = 1.4 for pulp and 1.3 for multiple products
	1974	Structural goals are to retain 18.4 m^2/ha (trees > 1.3 cm), residual max diameter of 50.8 cm, and q = 1.4.
	2008	Structural goal is to retain 16.1 m^2/ha (trees > 11.4 cm). Residual max diameter and q factor vary by species group.

[1] Study plans in 1953 and 1962 were written by T.F. McLintock. The 1974 study plan was written by Robert M. Frank, Jr. and the 2008 study plan was written by John C. Brissette and Laura S. Kenefic.

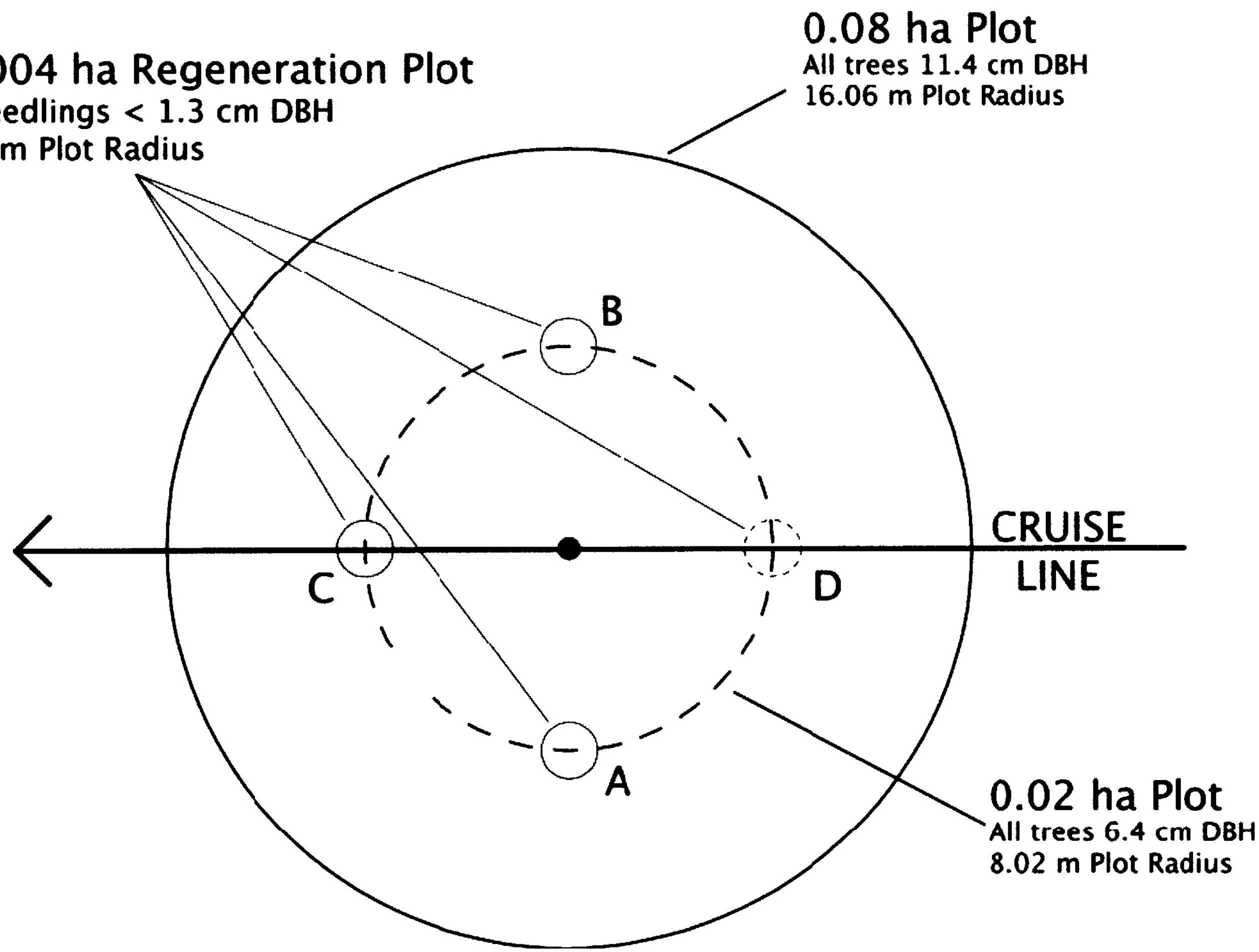

Figure 2.5. CFI plot design of the PEF prior to year 2000. Ingrowth into the sapling class (≥ 1.3 cm) is measured on the 0.02 ha plot. Milacre plot D was only found in the reference compartments (32A and 32B).

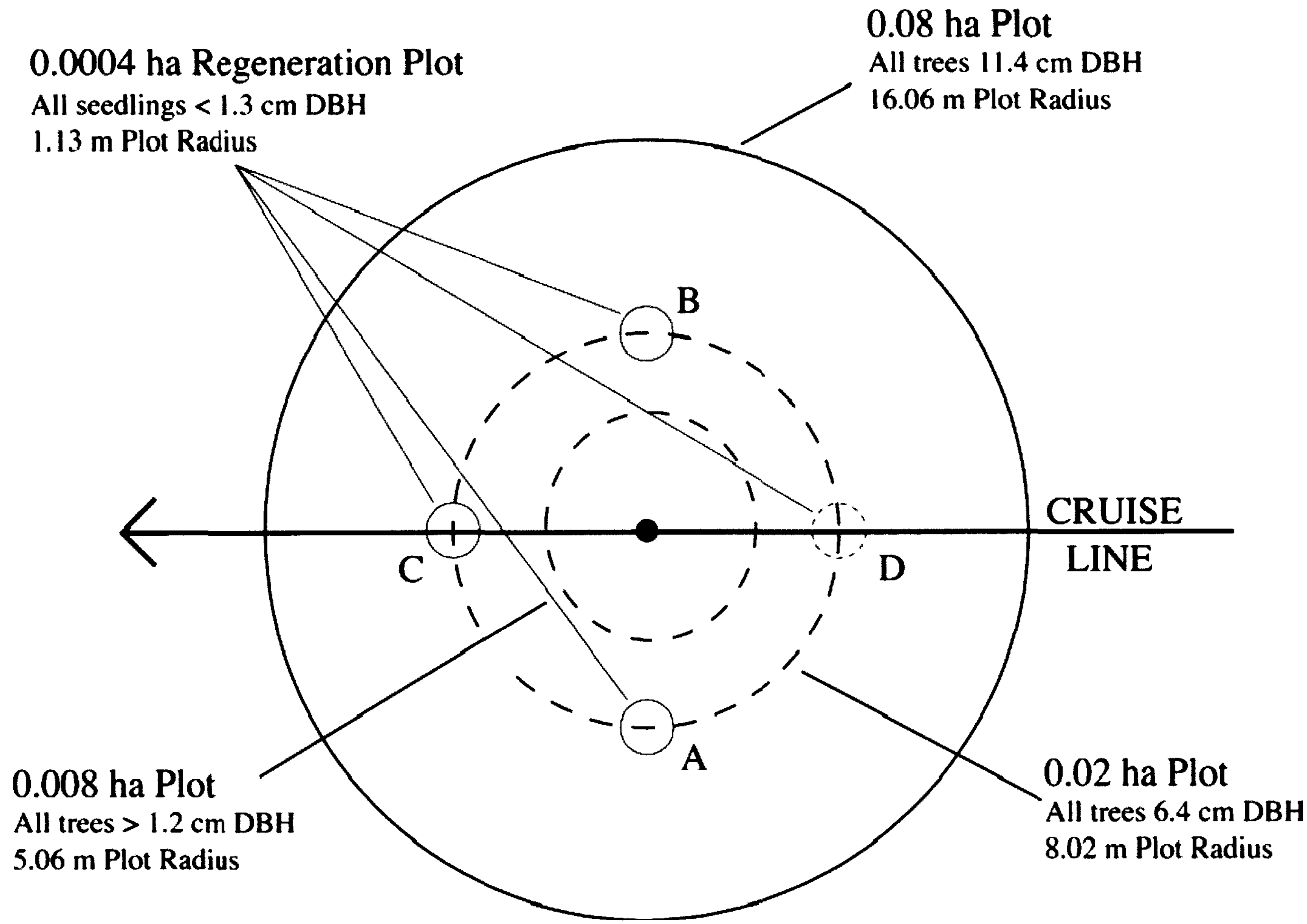

Figure 2.6. CFI plot design used on the PEF field season 2000 and after. Ingrowth into the sapling class (≥ 1.3 cm) is measured on the 0.008 ha plot. Plot D only found in the reference compartments (32A and

Table 2.3. Height classes of seedlings on regeneration plots of the PEF.

Class	Height
1	< 15.2 cm
2	15.2 cm – 30.5 cm
3	0.31 m – 0.61 m
4	0.62 m – 1.37 m
5	1.38 m – 1.2 cm dbh

DATA PREPARATION

The Forest Service's long-term compartment study dataset was used for this analysis. Tree numbering began in 1974; recruitment to the sapling class has been recorded since 1977. Recruitment, classified as trees not previously recorded and ≥ 1.3 cm dbh, are assigned a k (condition) code of 700. These trees were sorted by compartment, treatment, plot, and inventory and merged with regeneration data. All regeneration and recruitment data were assessed on a per-ha basis. Species were grouped according to shade tolerance (Table 2.4) using information provided by Burns and Honaka (1990).

Table 2.4. Species in each of the six species groups (Burns and Honkala 1990) and found in the regeneration and recruitment datasets for the PEF. Tolerance reference is ability to withstand shade.

Species Group	Abbreviation	Associated Species
Intolerant Softwoods	ISW	Tamarack (*Larix laricina*); Red pine (*Pinus resinosa*)
Tolerant Softwoods	TSW	Balsam fir; Spruce spp.; Eastern hemlock; Northern white-cedar
Intermediate Softwoods	INTSW	Eastern white pine
Intolerant Hardwoods	IHW	Paper birch; Gray birch; Trembling aspen; Bigtooth aspen; Black cherry (*Prunus serotina*); Balsam poplar (*Populus balsamifera*); Pin cherry (*Prunus pensylvanica*)
Tolerant Hardwoods	THW	Sugar maple; American beech; Eastern hophornbeam (*Ostrya virginiana*); American basswood (*Tilia americana);* Striped maple (*Acer pensylvaticum*); Mountain maple (*Acer spicatum*)
Intermediate Hardwoods	INTHW	White ash; black ash (*Fraxinus nigra*); Yellow birch; Red maple; Northern red oak (*Quercus rubra*)

STATISTICAL ANALYSIS

Statistical analysis was conducted with the R statistical program using the MASS, mvtnorm, coda, lattice, and pscl libraries (R Development Core Team 2008). Because the data were dominated by non-occurrence of ingrowth and had a hierarchical structure, a mixed-effects, zero-inflated model with a Poisson distribution and logit link was used to predict recruitment for different species groups. A zero-inflated model has two parts. First, the probability of recruitment occurring is modeled as a binary event. Second, the amount of recruitment is modeled, conditional on the outcomes of the first model.

Compartment and plot within compartment were treated as random. Average recruitment density per year, given that ingrowth occurred, was determined and used as the response variable; raw recruitment data were also graphed to observe trends. Regeneration in height class 5 for the previous inventory (inventory minus 1) was used as an explanatory variable predicting the density of recruitment at each inventory. Other explanatory variables used were: species groups, untransformed and transformed (natural log) of years since the treatment began, average treatment interval, silvicultural treatment, as well as interaction effects between years since the treatment began and treatment. Statistical significance was established at $\alpha = 0.05$. Average treatment interval was determined in the uneven-aged compartments (including the fixed diameter-limit) and the commercial clearcut (Table 2.5); number of years since the treatment began was used in lieu of average harvest interval in the reference and shelterwood treatments. Model assumptions including independence, normality and homoscedasticity of residuals were verified.

Table 2.5. Average harvest interval determined using harvest dates as described in the long-term PEF database.

Treatment	Average Harvest Interval (Years)
S05	5
S10	10
S20	20
FDL	22
CC	30
3SW	55
UC	55

Finally, residuals from the recruitment density model were assessed to investigate within-compartment variability. Depth to redoximorphic features (cm), also known as mottling, Briggs Site Class (Briggs 1994), which assesses soil drainage (site class 1 to 5 from well drained to very poorly drained respectively), and depth to water table (cm) were soil attributes examined. Other within-compartment variables included in the model assessment were overstory basal area, trees per ha, and distance from plot to compartment edge (m). Variance component analysis was conducted using the model factors to assess within-plot as well as between-factor variability. This was done using the R statistical program with the ape library (R Development Core Team 2008).

Results

DESCRIPTIVE DATA

Descriptive ingrowth data (Table 2.6) over our study period across treatments suggested that the highest average and maximum recruitment densities were in the CC treatments. This treatment also had the highest standard deviation (8,103 stems $ha^{-1}yr^{-1}$), varying from 0 to nearly 23,000 stems ha^{-1} yr^{-1}. Average ingrowth density appeared to be lowest in the S05 treatment, with an average of 1,323 stems ha^{-1} yr^{-1}. Variability was also least in this treatment, with a standard deviation of 1,323 stems ha^{-1} yr^{-1} and minimum and maximum numbers of stems ha^{-1} yr^{-1} of 0 and 5,281, respectively. The S05, CC, FDL and S10 treatments all had years with no ingrowth. The percentage of years measured where no ingrowth occurred is found in Table 2.7.

Periodic recruitment density by treatment and compartment is seen in Figures 2.7 and 2.8. In one of the UC compartments (Compartment 32A), there appears to be a peak in recruitment in year 1993. Compartment 32B, however, shows very little recruitment across all years. The CC compartments (8 and 22) show a peak of recruitment between

1992 and 1998. In the case of 3SW, there appear to be peaks in 1980 and 1990 (23B) and 1991 (29B). The FDL and SC compartments have steadier ingrowth, though there is a peak in S05 compartment 16 in 1996.

Table 2.6. Raw data attributes of ingrowth by treatment (1977-2009).

	Number of Ingrowth (# ha^{-1} yr^{-1}) by Treatment			
Treatment	**Mean**	**Standard Deviation**	**Min**	**Max**
3SW	4,789	5,826	8	14,674
CC	8,007	8,107	0	22,946
FDL	4,564	3,602	0	13,290
S05	1,323	1,323	0	5,281
S10	3,997	3,290	0	10,611
S20	5,390	4,654	8	12,820
UC	3,013	2,157	461	6,694

Table 2.7. Percentage of measurement years where no ingrowth occurred for five treatments on the PEF (1977-2009). Note: there were no years without ingrowth in the 3SW and S20 treatments.

Treatment	MU	Percentage of Years with no Ingrowth
CC	8	14%
	22	29%
FDL	4	17%
	15	14%
S05	9	22%
	16	33%
S10	12	0%
	20	25%
UC	32A	0%
	32B	40%

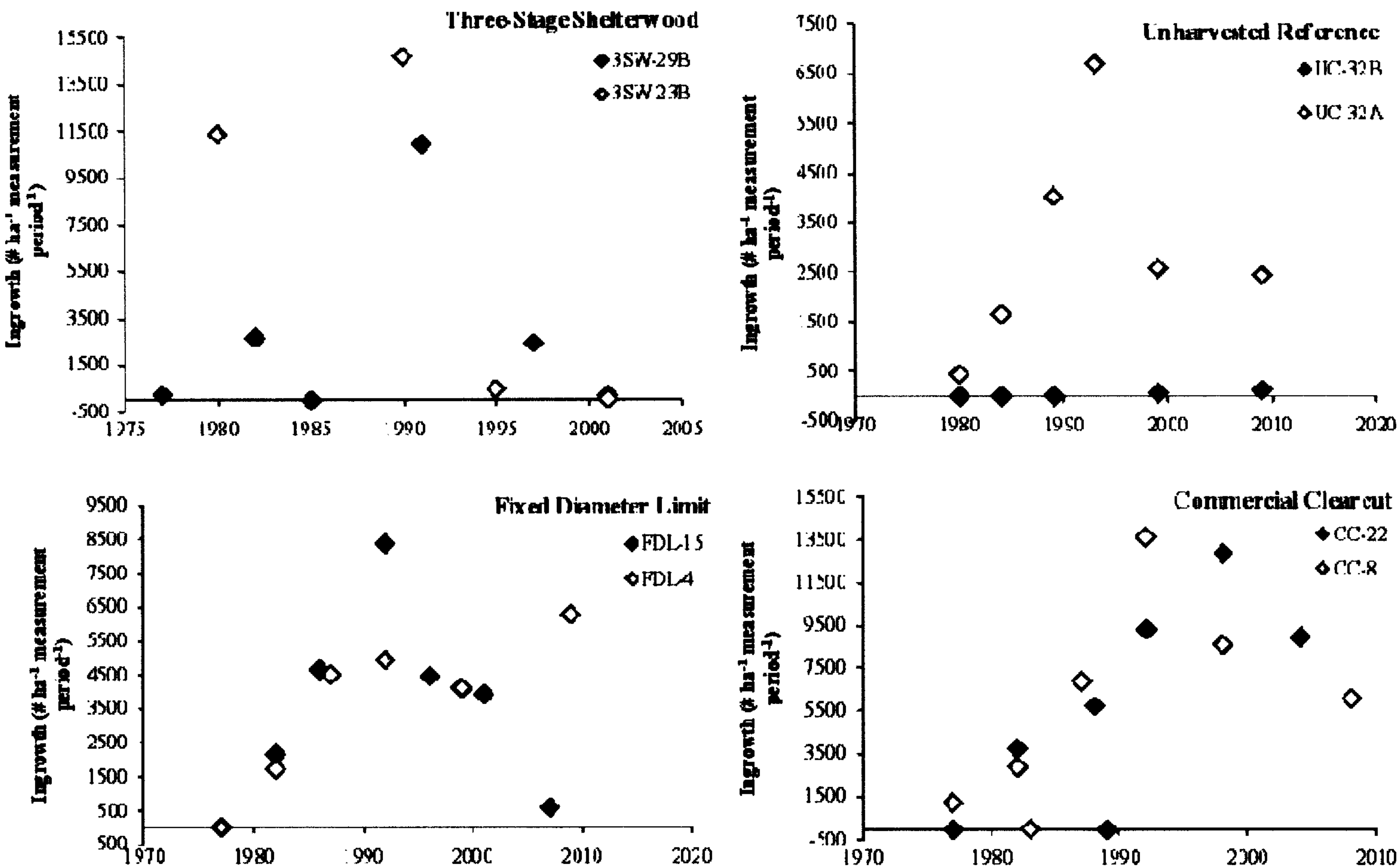

Figure 2.7. Average periodic ingrowth (# ha^{-1} measurement period^{-1}) for four treatments on the PEF.

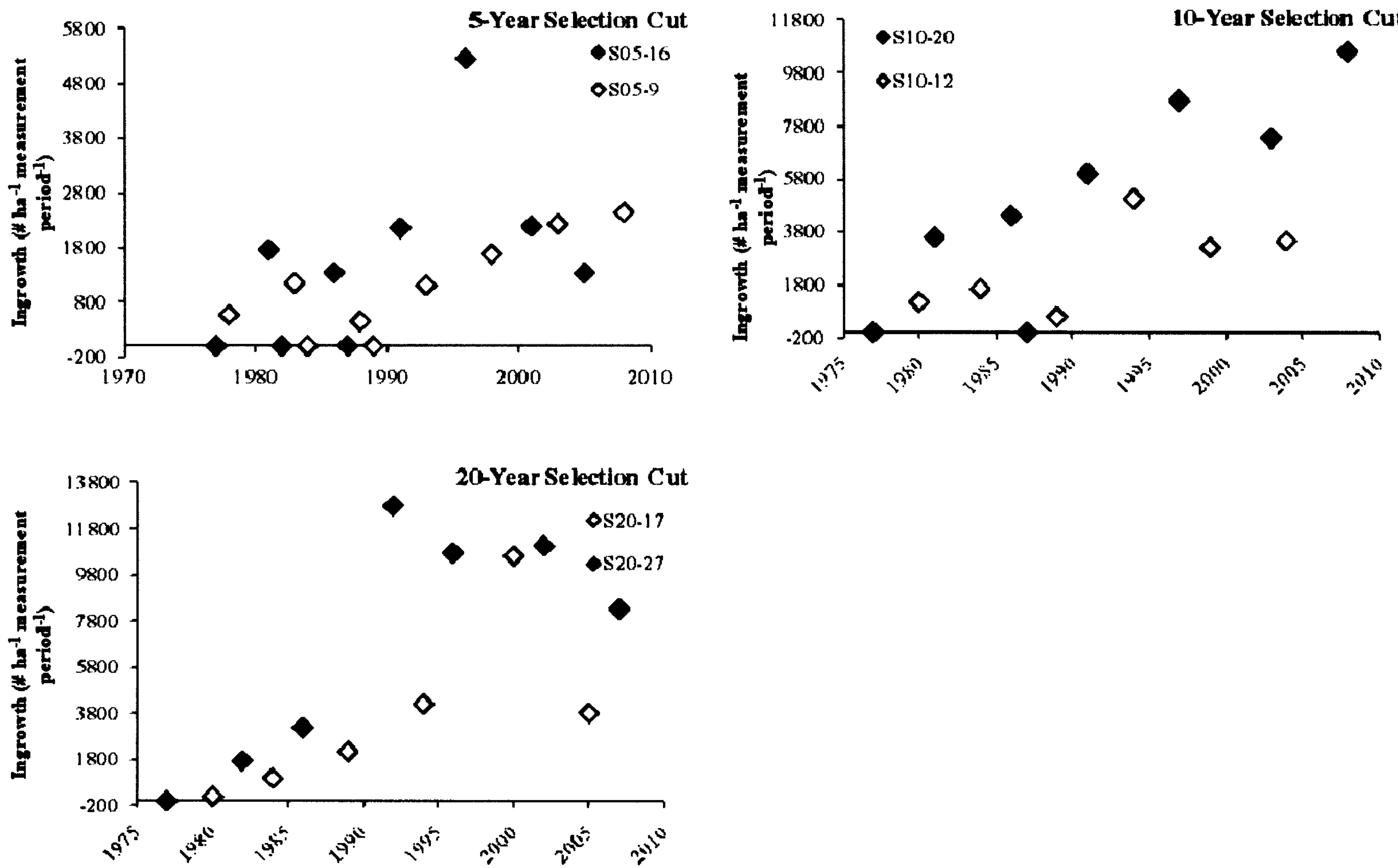

Figure 2.8. Average periodic ingrowth (# ha^{-1} measurement period^{-1}) for three selection silvicultural systems on the PEF.

PROBABILITY OF RECRUITMENT

Recruitment probability was modeled using a mixed-effects, zero-inflated model with a logit link for the binary data. The reference level for species groups was IHW. Results from this model show that the probability of periodic TSW recruitment is significantly different than IHW ($p < 0.05$). All other species groups were not found to be different from IHW ($p > 0.05$). The treatment reference level for the model was CC. The S05-years since treatment began (years) interaction was found to be significantly different from the CC-years interaction ($p = 0.0026$), however all other treatments and treatment-years interactions were not found to be different ($p > 0.05$). Time was determined to greatly influence the probability of recruitment and density given recruitment occurred. Years since treatment establishment and average treatment interval were both statistically significant factors determining probability of recruitment ($p < 0.05$) (Table 2.8).

When the significant model factors are used to predict the probability of recruitment through time, a few interesting trends are highlighted. First, higher probabilities of recruitment occur given longer harvest intervals of 30 years versus shorter 10-year intervals (Figure 2.9). Second, probability of recruitment peaked lower in TSW for both harvest intervals (0.78 and 0.90 respectively) as compared to the other species groups (0.84 and 0.92 respectively). However, declines in recruitment appear to be around the same post-harvest for both the 10- and 30-year intervals. Although treatment wasn't significant in this analysis, harvest interval implies different residual basal areas, based on the data used to construct the model. However, total BA was not found to be a significant factor with harvest interval in the model.

Table 2.8. Summary statistics found for probability of recruitment. Statistical significance was found at p-values < 0.05 for 95% confidence (bolded values). Reference level is IHW for species groups and CC for treatments.

Variable	Estimate	Standard Error	z value	Pr (>|z|)
Intercept	-12.3866	3.2412	-3.822	**0.0001**
IntHW	-0.0149	0.0985	-0.151	0.8800
IntSW	-0.0260	0.1578	-0.165	0.8689
ISW	0.2722	0.4751	0.573	0.5667
TSW	-0.2912	0.0840	-3.466	**0.0005**
THW	0.1428	0.2192	0.652	0.5147
Years:TrtFDL	0.0400	0.0294	1.363	0.1730
Years:TrtS05	0.0888	0.0294	3.014	**0.0026**
Years:TrtS10	0.0160	0.0303	0.526	0.5986
Years:Trt3SW	0.0066	0.0306	0.215	0.8300
Years:TrtS20	0.0271	0.0293	0.924	0.3554
Years:TrtUC	-0.0484	0.0468	-1.034	0.3011
FDL	-0.1409	0.8290	-0.170	0.8650
S05	0.2136	0.8190	0.261	0.7944
S10	1.2640	0.8386	1.507	0.1317
S20	0.4780	0.8238	0.580	0.5618
3SW	-0.6845	0.8980	-0.762	0.4459
UC	2.1383	1.6113	1.327	0.1845
Years	-0.4832	0.0545	-8.867	**< 0.0001**
log(Years)	7.6314	1.2947	5.894	**< 0.0001**
Harvest Interval	0.0590	0.0126	4.695	**< 0.0001**
log(HtClass5 + 0.01)	-0.0091	0.0063	-1.449	0.1472

Table 2.9. Summary statistics for density of recruitment, given its occurrence. Statistical significance was found for p-values < 0.05 for 95% confidence. Reference level is IHW for species groups and CC for treatments.

Variable	Estimate	Standard Error	z value	Pr (>|z|)
Intercept	-1.72e+01	2.55e-01	-67.507	< 0.0001
IntHW	3.45e-01	8.97e-03	38.462	< 0.0001
IntSW	-5.52e-01	1.87e-02	-29.45	< 0.0001
ISW	-1.12e+00	6.30e-02	-17.82	< 0.0001
THW	-2.70e-01	2.30e-02	-11.783	< 0.0001
TSW	7.71e-01	7.27e-02	106.087	< 0.0001
Years:FDL	1.53e-02	9.77e-04	15.645	< 0.0001
Years:S05	3.83e-03	9.88e-04	3.875	0.0001
Years:S10	3.77e-02	8.56e-04	4.399	< 0.0001
Years:S20	2.03e-02	9.42e-04	21.589	< 0.0001
Years:3SW	-6.62e-02	1.32e-03	-50.312	< 0.0001
Years:UC	-1.59e-02	1.46e-03	-10.881	< 0.0001
FDL	-8.53e-01	4.25e-02	-20.085	< 0.0001
S05	-9.69e-02	4.97e-02	-1.948	0.051
S10	2.13e-01	4.27e-02	4.999	< 0.0001
S20	-8.02e-01	4.22e-02	-18.983	< 0.0001
3SW	3.06e+00	5.23e-02	58.631	< 0.0001
UC	5.37e-01	6.16e-02	8.708	< 0.0001
Years	-1.70e-01	2.57e-03	-66.142	< 0.0001
ln(Years)	7.45e+00	9.64e-02	77.264	< 0.0001
Harvest Interval	1.30e-02	8.78e-04	14.811	< 0.0001
ln(HtClass 5+0.01)	4.20e-02	5.21e-04	80.481	< 0.0001

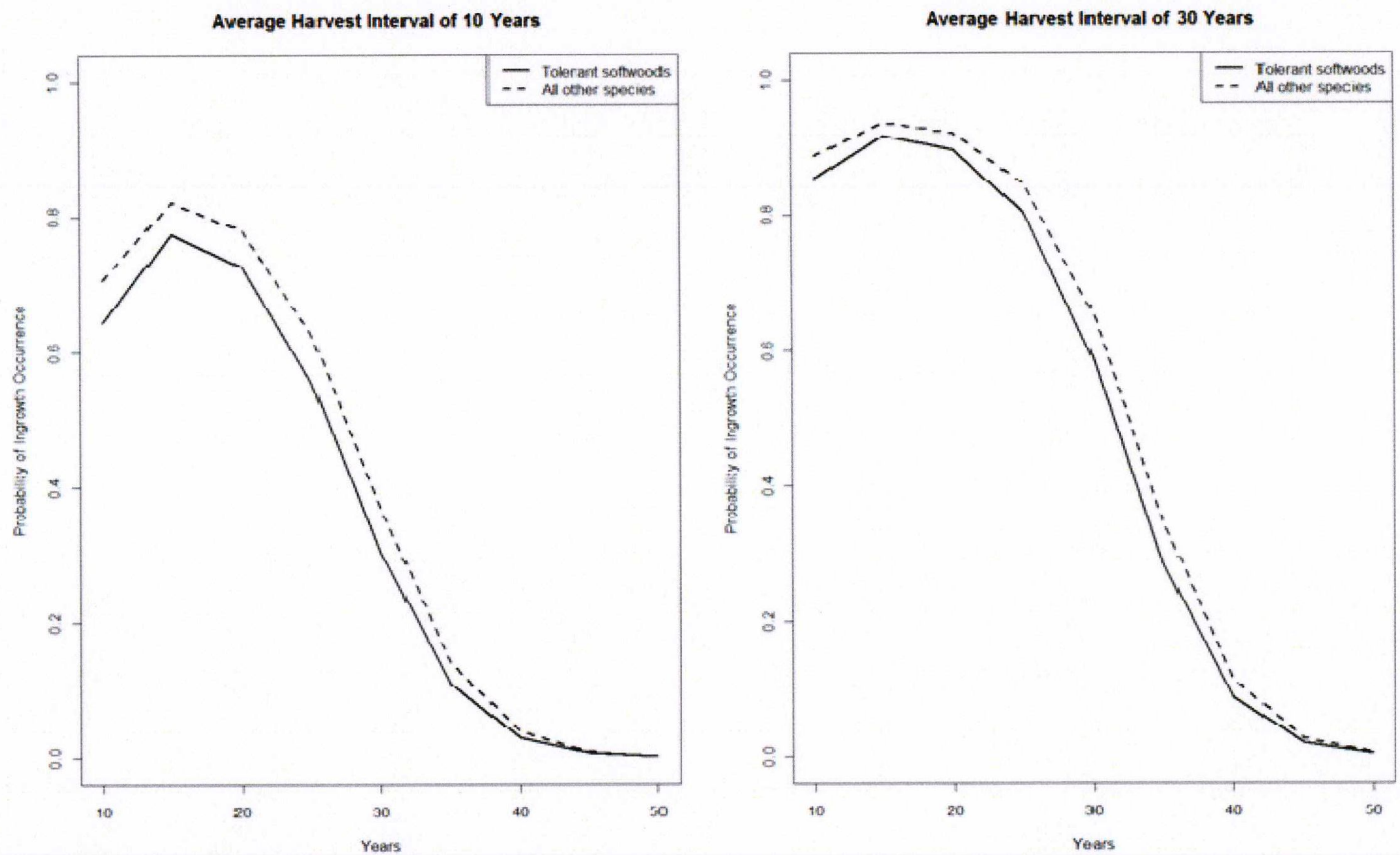

Figure 2.9. Probability of periodic ingrowth occurrence predicted for tolerant softwoods and all other species for 10- and 30-vear harvest intervals.

DENSITY OF RECRUITMENT

Summary statistics for average annual density of the recruitment given that recruitment occurs may be seen in Table 2.7. This model was used to predict general trends in density of recruitment across treatment and species groups (Figure 2.10). Density of recruitment was found to show sigmoidal-shaped curves and be quite variable across species groups and treatment. The TSW and IntHW groups were found to have the highest average annual ingrowth densities, ranging from 100 to 220 and 60 to 150 stems ha^{-1} yr^{-1}, respectively. TSWs peaked at 220 stems ha^{-1} yr^{-1} in the 3SW around 38 years after the treatment began. ISWs were not present in all treatments and exhibited very low ingrowth densities ranging from 0 to 30 stems ha^{-1} yr^{-1}. THW, IHW, and IntSW groups had ingrowth densities ranging from approximately 30 to 120 stems ha^{-1} yr^{-1}.

Ingrowth density was greatest across all species groups in the 3SW, except IntHW, which was greatest in S20. Lowest ingrowth densities were found in S05 (Figure 2.9). The FDL and S10 treatments also had low ingrowth across all species groups. There appears to be a lag of 30 to 40 years from the time of study initiation to highest densities of recruitment.

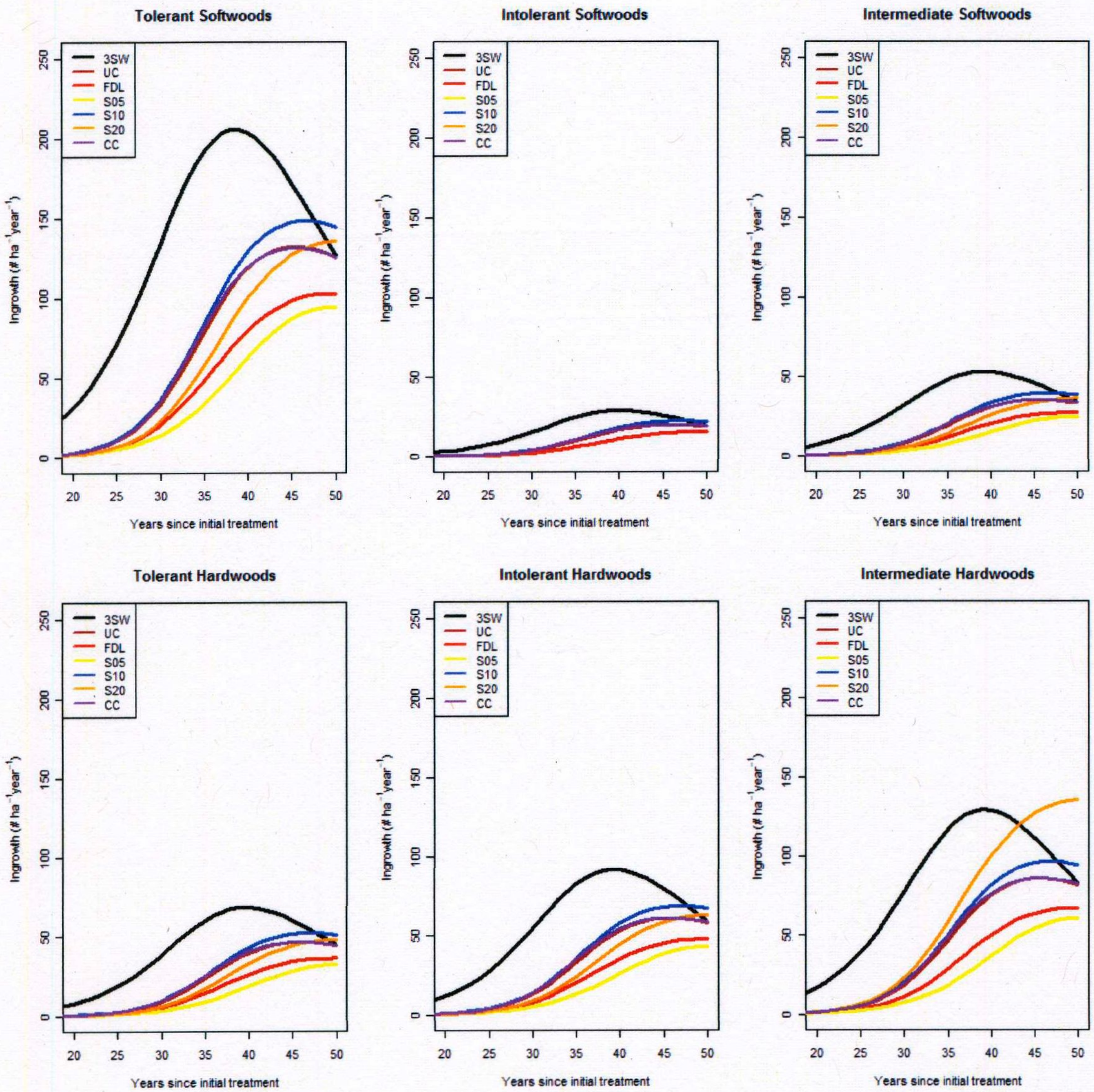

Figure 2.10. Predicted ingrowth density (stems ha^{-1} year^{-1}) over seven treatments and six species groups on the Penobscot Experimental Forest in Bradley and Eddington, Maine.

VARIANCE COMPONENTS

Figure 2.11 is a variance component analysis where Plot, MU, Years since the treatment began, Trt (treatment), and species group represent independent factors in the recruitment density model, and shows the amount of variance contributed by each factor. Species group and Trt account for the smallest percentage of variance within the model, whereas years since the treatment began, and compartment contribute a modest amount of variance. The primary source of variance is within-plot over time (i.e., remeasurements of the same CFI plots).

Residuals from the recruitment density model were plotted against plot-level variables (Figure 2.12) and used as model verification. Basal area ($m^2\ ha^{-1}$), trees per ha, distance from plot to compartment edge, depth to redoximorphic features, depth to water table and Briggs site class were all used to determine if these plot-level variables created a pattern in the residuals, which would indicate the recruitment model was potentially missing a significant independent factor. All residuals in each graph appear scattered around zero and random in nature. Lowess regression lines (in red) indicate that there is no trend in the variables assessed.

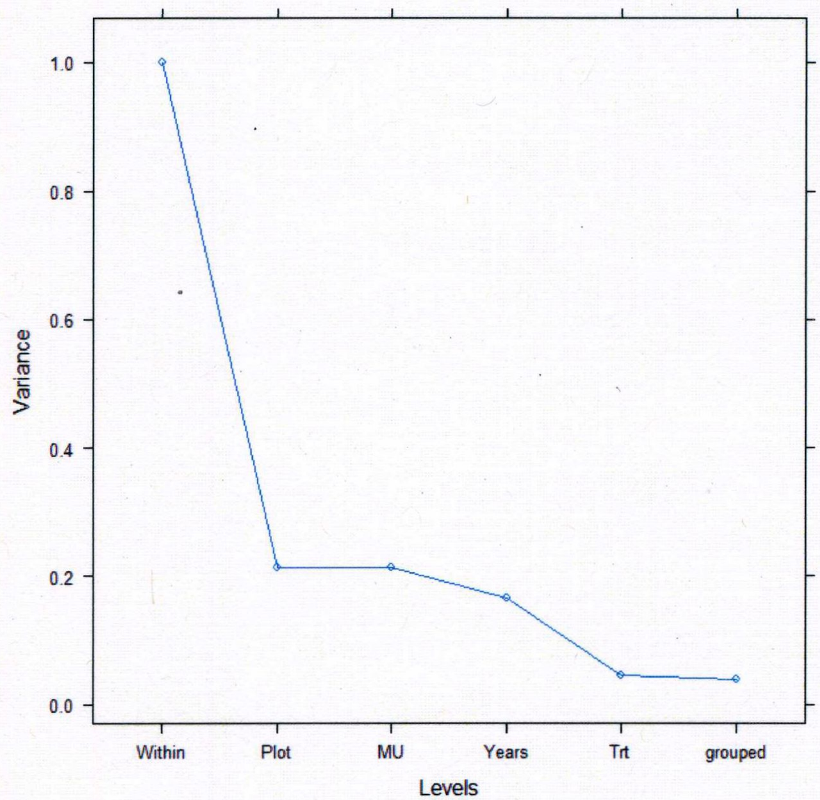

Figure 2.11. Within plot and between factor variance found for the recruitment density data. "Years" represents years since the treatment began. "Grouped" represents species tolerance groups and "Trt" represents treatment.

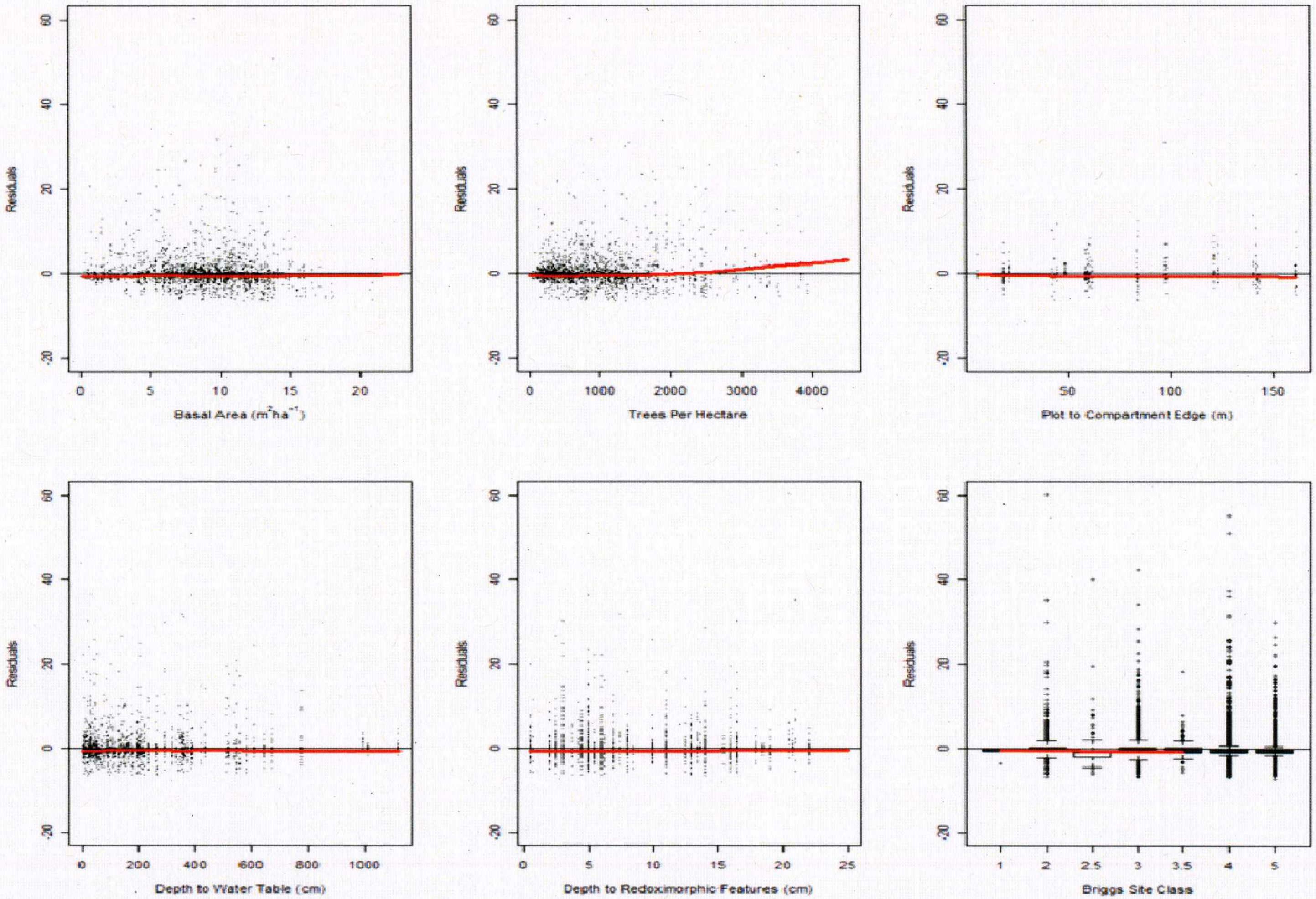

Figure 2.12. Residuals (# ha^{-1} yr^{-1}) from the recruitment density model plotted against plot-level variables.

Discussion

PROBABILITY OF RECRUITMENT

The probability of ingrowth occurring during an inventory period was assessed relative to factors such as species group, treatment, years since the treatment began, years between treatments, and amount of regeneration present. General outcomes from this model indicate that time since the treatment began has the greatest influence on probability of recruitment. Species and treatment had no significance in this analysis, however the TSW species group was found to be significantly different (lower) than the other groups.

Tolerant softwoods are the defining species group of the northern mixed-conifer forest. In stands such as these where rainfall is abundant, regeneration failures are not common (Seymour 1992); however, sapling recruitment is variable (Table 2.4) and dependent on a number of factors. TSW had a lower probability of ingrowth than other species groups. Because these species tend to remain in the understory for long periods of time prior to release (Weaver 2007) and advance regeneration is often necessary to outcompete faster-growing species (Seymour 1992), this finding is not unexpected.

Treatment was generally not found to have significance when determining probability of recruitment. All possible pairwise comparisons were not made for the years since the treatment began and treatment interaction, however the S05-years interaction was found to be significantly different than CC-years (Table 2.5). Although significant in the analysis, the overall effect of this interaction is small (1-3%). This suggests that there may be other recruitment differences in treatments over time. Because S05 has been subjected to frequent, light removals leaving a residual basal area of 24.1 $m^2 ha^{-1}$ greater than 11.4-cm dbh it is likely that recruitment in this treatment is gradual in comparison to heavier treatments or unregulated harvesting. In a 20-year study conducted on the PEF, Kenefic and Brissette (2005) found that species composition of sapling ingrowth did not differ by treatment for selection cutting and diameter limit compartments, however within-treatment variability is common at the PEF (Sendak et al. 2003).

Recruitment into the sapling class is highly dependent on factors such as years since the treatment began and treatment intensity and frequency, which oftentimes determine stand structure and light availability. Table 2.5 shows that the years since the treatment began and average harvest interval are both significant factors determining probability of ingrowth. Since these factors were significant in predicting the probability of recruitment in this model, long-term studies, especially under uneven-aged management may be required in order to gain a full perspective on recruitment trends.

DENSITY OF RECRUITMENT

Assuming recruitment occurred, most factors assessed were found to be significant predictors of the density of recruitment. Amount of regeneration in the largest height class, for example, was not a significant predictor of probability of ingrowth ($p = 0.15$), but was a significant predictor of the density of ingrowth given its occurrence ($p < 0.05$) (Tables 2.5 and 2.6). This means that although the amount of regeneration in the largest height class did not influence the probability of an individual stem recruiting, the greater the amount of regeneration, the higher the density of recruitment on the plot would be in the following inventory. All species groups and time factors were also significant. S05 was found to not be different from the reference level (CC) in terms of the amount of recruitment, given that it occurred. All other treatments' densities of recruitment were statistically different from the CC. Other pairwise comparisons were not conducted.

Shade-tolerant seedlings tend to remain in the understory for long periods of time and may experience rapid growth following one or more periods of release (Weaver, 2007). Which seedling becomes recruited is highly dependent on a number of factors that operate both on fine and broad scales. Kenefic et al. (in review) found that sapling recruitment was inversely related to relative density of the overstory (trees ≥11.4 cm dbh). Furthermore, age may also negatively impact the future stand-level production by decreasing growth efficiency of shade-tolerant conifers which occupy the understory for long periods of time (Seymour and Kenefic 2002).

Although Olson (2009) found mixed hardwood regeneration was becoming more abundant in the long-term study on the PEF, densities of TSW recruitment exceeded those of any other species group. Figure 2.10 shows that maximum densities of TSWs exceeded those of THWs, IHWs, and IntHWs by nearly four-, three- and two-times, respectively. This is not surprising, given that the study stands are composed mainly of tolerant softwoods (Fig. 2.3).

Because all shade-tolerant species were grouped together in this study, we do not have an accurate assessment of how well individual species are represented. For example, a key question for shade tolerant species is how is spruce is doing in comparison to hemlock and balsam fir? Although all tolerant softwoods had considerable amounts of ingrowth given the model, one species may be out-performing another by recruiting into the sapling class more prolifically. Assessment of sapling recruitment by species for each of the dominant northern conifers (balsam fir, red spruce, and eastern hemlock) over the study period suggests that this is the case (Figure 2.13). These data also illustrate that red spruce ingrowth is far greater in the 3SW than other treatments and that overall tolerant softwood recruitment in this treatment is greater than other treatments. Though recruitment density varies over time and among treatments, the relative amount of red spruce is consistently low.

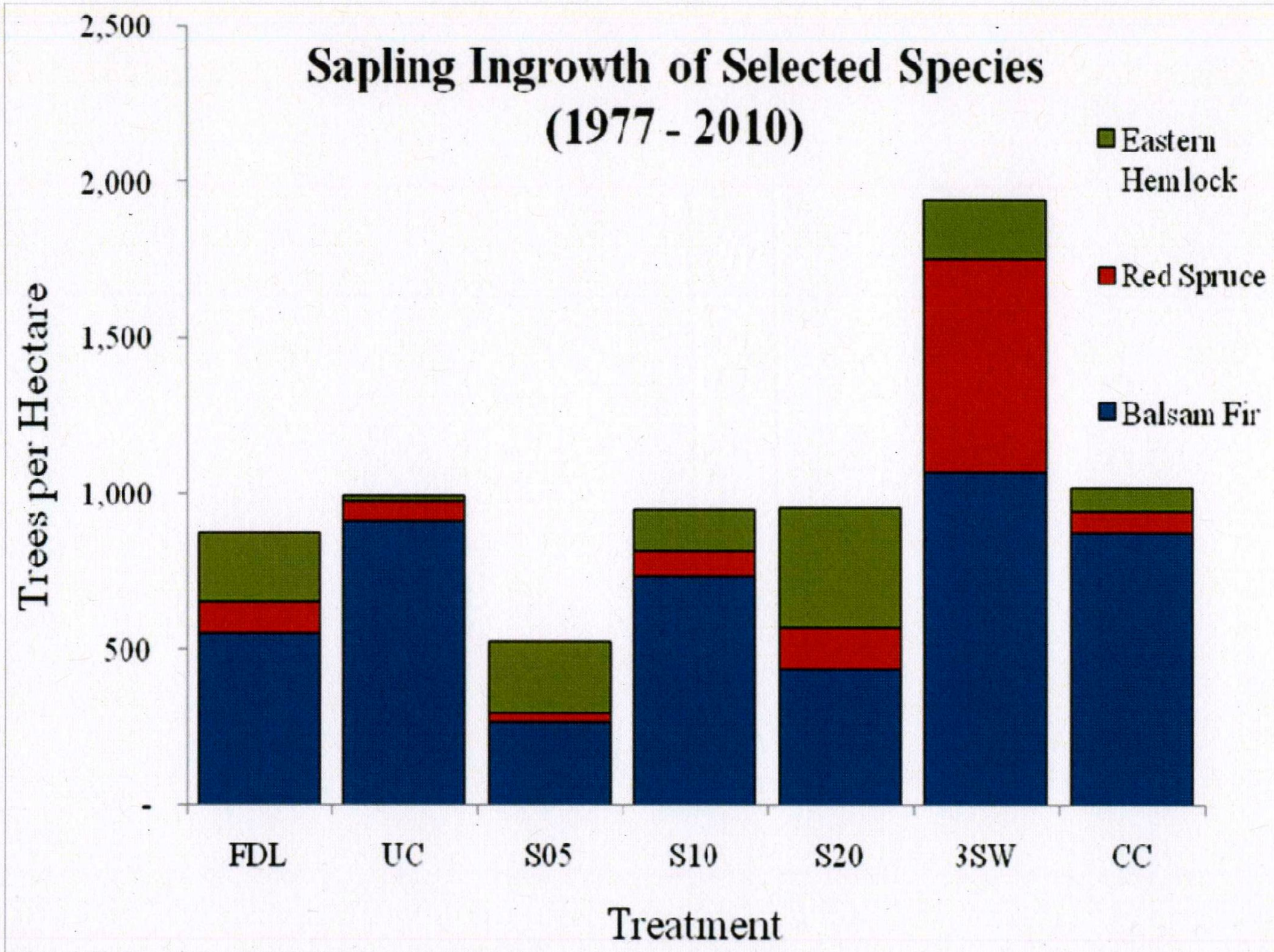

Figure 2.13. Cumulative ingrowth (trees per ha) since 1977 by treatment for three tolerant softwood species. Figure adapted from Robert Seymour, University of Maine; data provided by the U.S. Forest Service.

All treatments, except S05, were found to be significantly higher than CC when investigating average annual density of recruitment, given its occurrence. This is consistent with raw data (Table 2.5), which show lower average recruitment densities in S05 than all other treatments. The 3SW has the highest recruitment density across all species, except IntHWs. Since the 3SW treatment was designed to enhance desired species including tolerant softwoods such as red spruce (Sendak et al. 2003), this finding is expected. In the present study, we found that almost all species had higher recruitment densities in the 3SW than all other treatments. However, all of this ingrowth peaked as other treatments continued to rise in ingrowth.

Number of years since the treatment began and treatment interval are both important factors which contribute to the density of recruitment. In most cases, 30 years since the treatment began were required in order for recruitment densities to begin increasing. Because sapling recruitment was not measured in the first 20 years of the experiment, we cannot rule out earlier peaks in recruitment, though that seems unlikely. Long seedling stages and slow growth in new recruits on the PEF (1 cm over 3-5 years) (Kenefic et al. in review), may indicate that the 55 years of silvicultural treatment may not be long enough to evaluate long-term sapling ingrowth trends. Because recruitment was quicker to initiate in the 3SW, peaking around 40 years after the treatment began for all species groups, this may not be the case for even-aged management. Because the 3SW is even-aged, it is expected that all recruitment will happen over a short period of time. In selection stands, recruitment happens consistently over time. This may explain the lack of decline in recruitment densities for the uneven-aged stands.

Trends are similar in the UC compartments; this may reflect the condition of the forest the when the experiment was established. The spruce budworm outbreak of the early 1920s may have created a large amount of mortality in the stands which would have acted like a harvest or treatment. Although compartment 32B had very little ingrowth throughout time, 32A had a gradual climb in recruitment, peaking in 1995 prior to falling (Figure 2.7).

VARIANCE COMPONENTS

Variance component analysis conducted on the recruitment model indicated that there was high within-plot variability. Weaver (2007) found that northern conifer seedlings in selection stands may reach 30 or 40 years of age before reaching 0.5 meters in height. This indicates that growth dynamics of seedlings may be more reliant on site specific factors, some of which were considered in this chapter. Figure 2.10 shows that approximately 80% of the variance in the model may be accounted for by within-plot factors. This is consistent with other research findings on the PEF (Sendak et al. 2003; Kenefic and Brissette 2005; Kenefic et al. (in review)).

When individual variables were assessed by plotting model residuals (Figure 2.11), it does not appear that these factors are influencing the residuals or creating any patterns which would lead to significance or high influence in recruitment rates. Soil attributes, including depth to water table, depth to redoximorphic features and Briggs Site Class did not account for the variance, nor did distance to compartment edge, basal area or trees per hectare. However, the latter variables may be implicit in the treatment factor.

Recruitment is stochastic and there may be many factors which contribute to its occurrence, not captured by higher-level variables used in this model. Therefore, there are other plot-level factors which have not yet been considered which are significantly influencing sapling recruitment on the PEF. Local site quality and attributes including down woody debris, timing of harvests in regard to seed year, and browsing may be local factors which should be considered more closely.

LIMITATIONS

Due to the high number of factors and significant interactions, all possible pairwise comparisons were not made. This means that there may be differences between factors which were not assessed and may be of interest in future analyses. In addition, in the probability of recruitment analysis, measurement intervals were not equal, ranging from 3.2 to 10.0 years with an average of 4.9 years. Because periodic instead of cumulative ingrowth was analyzed, ranges in total recruitment over the study period were not assessed. Because both even- and uneven-aged treatments were assessed in this analysis, it was believed that periodic ingrowth was the most appropriate method of calculating recruitment. This allowed evaluation of treatment differences, but may have shown different results, had cumulative recruitment been measured.

Conclusions

This study was conducted because there is limited understanding of recruitment trends in the Acadian Forest. Future forest conditions must be measured not only by what species are regenerating, but by what species are able to reach the sapling class and eventually become part of the overstory. For this reason, understanding the dynamics between the seedling and sapling class is a vital part of forest management. This study has shown that recruitment into the sapling class depends on a number of factors.

Average annual recruitment in uneven-aged treatments gradually increased through time and never reached a full "peak" state, indicating that recruitment occurred consistently as partial overstory removals took place. Heavier harvests as in the shelterwood compartments resulted a peak in recruitment and a decline associated with stem exclusion. As was predicted from the model, recruitment in the shelterwood compartments had already begun to decline as other compartments were gradually increasing in recruitment density.

Management goals in northern mixed conifer forests often aim to increase tolerant conifers and decrease intolerant hardwoods. In this study tolerant conifers reach the highest densities in the 3SW, however also reach high densities near 150 stems (ha^{-1} yr^{-1}) under the 10- and 20-year cutting cycles of selection management. Intermediate hardwoods are prevalent in the 3SW as well, however tolerant conifers are greater (ha^{-1} yr^{-1}) by over two-fold. Intolerant and intermediate hardwoods are primarily found throughout unregulated harvesting operations such as in the CC and FDL. Though species-specific analysis was not conducted, data suggests spruce is a small proportion of the recruitment, and best under the 3SW.

There are many factors influencing recruitment dynamics following disturbance. In managed forests, type of treatment, including frequency of harvest and residual BA are driving factors affecting periodic ingrowth, however there are other factors which should be considered. Site conditions varying spatially across and within treatments also influence the rate at which seedlings accumulate height. Browsing, seed years, down woody debris, and land use history are a few examples of factors which should be assessed to determine what other variables influence recruitment.

Partial disturbances in the region and shade-tolerant species' ability to persist in the understory for long periods of time prior to release creates a complex management environment. This, as well as the numerous stand- and plot-level factors which must be considered when managing to promote recruitment, make managing forests in the Northeast difficult. Management as in the 3SW which allows tolerant conifers to becomes established prior to release or those that follow natural disturbance regimes in northern mixed-conifer forests including light harvests (Seymour et al. 2002) would promote conifer-dominated stands by creating enough shade to prevent hardwood dominance. Release treatments may be required (Weaver 2007, Larouche 2010) in order to ensure sufficient sapling recruitment of target species (e.g. spruce).

CHAPTER 3

SEEDLING HERBIVORY IN THE ACADIAN FOREST OF EAST-CENTRAL MAINE

Introduction

Natural disturbances and forest management activities such as timber harvesting produce changes in forest composition and structure that affect wildlife – habitat relationships. Spruce budworm (*Choristoneura fumiferana*) outbreaks, for example, cause periodic mortality of balsam fir (*Abies balsamea*) and spruce (*Picea* spp.) throughout the Acadian region, and result in increased forest heterogeneity. Newton et al. (1989), reported that wildlife such as snowshoe hare (*Lepus americanus*), moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) are adapted to these natural dynamics. Harvesting also creates a mosaic of forest developmental stages, which offer varying abundances and species of browse (Newton et al. 1989). These favor different wildlife species, which in turn exhibit varying browsing pressures on the forest. White-tailed deer, for example, commonly utilize forest edge and the early-successional habitat associated with gaps in the canopy, as well as grassy openings within mature forests (Waller and Alverson 1997). Hare also require early successional habitat, such as 10-15 year old clearcuts, which provide browse as well as low cover (Jakubus 2002). Moose, however, are often found in predominately clearcut forest matrix, which provide forage and nearby winter cover areas (Monthey 1984). Because herbivory can be an important influence on the growth and development of young trees (e.g. Larouche et al. 2010), understanding relationships between browsing and forest structure and composition is critical to sustainable forest management in areas with high herbivore populations.

Herbivores such as deer, hare, moose, and small rodents are common in central Maine and are found on the Penobscot Experimental Forest (PEF) (Blum 1977; Larouche et al. 2010). Although these animals have not been surveyed on the PEF, the Maine Department of Inland Fisheries and Wildlife (MDIFW) reports that there are currently 6 - 8 deer per square ha in central Maine (Larouche et al. 2010). Because herbivores have plant species preferences, herbivory has the potential to prevent certain tree species from recruiting to larger size classes. Lautenschlager (1997) found that when available, moose prefer hardwood browse, but will shift to conifers and even red spruce (*Picea rubens*) in the late winter. A study in north-central Maine found that 71% of the winter diet of moose is balsam fir and that 35% of the winter diet of white-tailed deer is white spruce (*Picea glauca*) (Ludewig and Bowyer 1985). Significant browsing can decrease seedling growth capabilities and change stand development patterns (Krueger et al. 2009). Negative effects of browsing on seedlings have been found to be much greater than those of browsing on mature trees (Swaihart and Picone 1998; Kozlowski 1971). Browsing can compromise a seedling's ability to compete for resources; Blum (1977) found that average growth was significantly different between browsed and unbrowsed balsam fir on the PEF.

In Maine, balsam fir is considered important winter forage for moose (Joyal 1976; Ludewig and Bowyer 1985; Peterson 1955; Prescott 1974; Rounds 1981), but a last resort for white-tailed deer (Banasiak 1961; Ludewig and Boyer 1985; Peterson 1955). This is contrary to a study on Anticosti Island in the Gulf of St. Lawrence, which found that balsam fir stands decreased in area from 40% to 20% after the introduction of deer, though there were only three species of browse available (white spruce, black spruce (*Picea mariana*), and balsam fir) (Sauve and Cote 2007). McLaren (1995) found balsam fir to be preferred by moose on Isle Royal and that repeated browsing, while creating growth suppression, also conditioned plants to have higher resistance to future browsing.

Though balsam fir and red spruce are characteristic of the Acadian Forest, other species including eastern hemlock (*Tsuga canadensis*), northern white-cedar (*Thuja occidentalis*), and mixed hardwoods are common. The early stages of growth are critical to the development and survival of eastern hemlock (Olson et al. 1959; Anderson and Loucks 1979) and seedlings often succumb to heavy browsing pressure in areas with high deer populations (Swift 1948; Lorimer 1996). Regeneration may fail due to browsing (e.g. Frothingham 1915; Stoeckler et al. 1957), which reduces the number of seedling and sapling recruits (Anderson and Katz 1993). Northern white-cedar seedlings and saplings are an important source of winter browse for deer and moose, and recruitment failures are common throughout the region (Hofmeyer et al. 2007). Larouche et al. (2010) recently found that northern white-cedar seedlings and saplings have been preferentially disfavored by deer browsing on the PEF.

Long-term field observation on the PEF suggests browsing is considerable and likely important, even for less-palatable species like the spruces. For example, an experimental trial with <1-year-old planted red spruce and balsam fir seedlings suggested that spruce were preferentially browsed by hare, though these results were preliminary (Kropp 2007). However, little research has been done on the probability and severity of browsing in the Acadian region, or on the PEF specifically. Relationships between browsing and stand structure and composition are of interest, because they inform our understanding of stand dynamics under a range of silvicultural treatments. Specific objectives of this study were:

(1) to determine the probability of browsing occurring given the silvicultural treatment, species of seedling, and height class of seedling;

(2) assess the average damage (expressed as 1-5 based on percentage of foliage removed) to seedlings caused by browsing, by seedling species, compartment (i.e., stand) and animal group (deer/moose or hare/rodent);

(3) given the occurrence of browsing, assess the severity (percentage of seedlings browsed) at the plot level.

Methods

STUDY SITE

The 1680-ha PEF is located in the towns of Bradley and Eddington, Maine in Penobscot County (Figure 3.1). The PEF is part of the mixed northern conifer forest, which extends from southeastern Canada and Maine to the Adirondack Mountains of New York, comprising an ecotone between boreal and eastern broadleaf forests (Sendak et al. 2003). The forests are characterized by a mixture of conifer species and northern hardwoods in varying amounts depending on a number of different factors including climate, aspect, elevation, and site quality. The Acadian Forest (Rowe 1972) of central Maine and adjacent Canada is typically dominated by red spruce, white spruce, eastern hemlock and balsam fir with varying amounts of northern hardwoods including trembling aspen (*Populus tremuloides*), bigtooth aspen (*Populus grandidentata*), paper birch

(*Betula papyrifera*), yellow birch (*Betula alleghanensis*), American beech (*Fagus grandifolia*), red and sugar maple (*Acer rubrum* and *Acer saccharum*) and cherry (*Prunus spp.*). Other species that are commonly present are eastern white pine (*Pinus strobus*) and northern white-cedar.

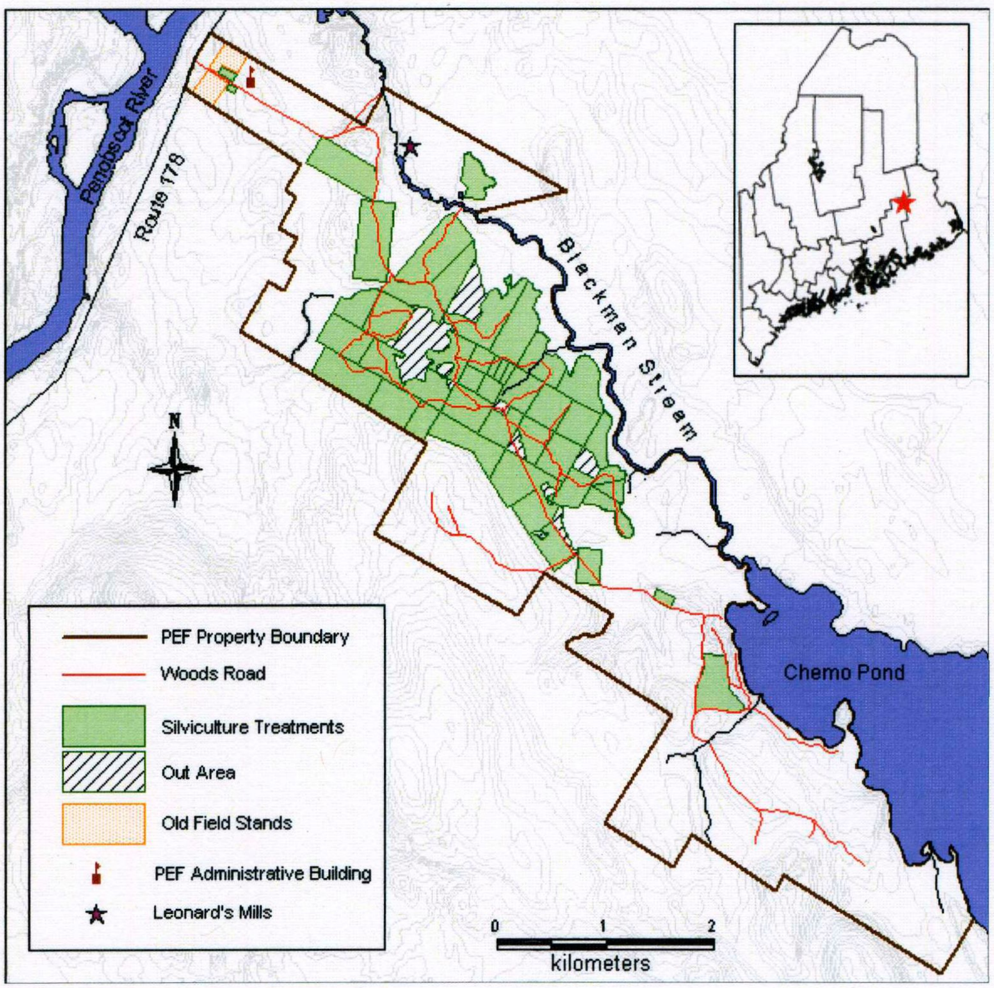

Figure 3.1. Map of the Penobscot Experimental Forest (Bryce 2009).

Soils on the PEF are Wisconsin glacial till derived from fine-grained sedimentary rock and tend to be thin, shallow, wet spruce-fir flats. Glacial till ridges are well-drained stony and Plaisted loams and moderately well-drained sandy and Howland loams. Flat till areas located between ridges are comprised of poorly and very poorly drained silt, Monarda and Burnham loams (Safford et al. 1969). Climate in central Maine is cool and humid. Mean annual temperature is 6.6° C and average precipitation is 106 cm. The growing season is approximately 160 days.

Land use history of the area prior to establishment of the PEF in 1950 is not well documented. The forest appeared to be irregular in age and size structure when the land was purchased. Descriptions of the area that would become the PEF were recorded on maps in the 1920s and 1940s (on file with the U.S. Forest Service). The study area was described in 1929 as "mixed softwood second growth" with pole-size spruce and fir, hemlock up to sawtimber size, scattered hardwoods and good spruce and fir regeneration and as "operable spruce-fir-hemlock" in 1949. These conditions were most likely a result of natural stand development and a long history of periodic partial cutting (Sendak et al. 2003; Kenefic et al. 2006). Large-scale, stand-replacing natural disturbances are uncommon in the Acadian region and have a return interval of 250-800 years (Lorimer 1977), although small-scale, gap-forming disturbances and periodic spruce budworm outbreaks (most recently in the 1970s and 1980s) are common (Seymour et al. 2002).

The PEF is unique because it is a long-term research site containing twice-replicated silvicultural treatments on 170 ha, established by the U.S. Forest Service between 1952 and 1957 (Sendak et al. 2003). Treatments included in this large-scale "compartment" study include: the selection system on 5-, 10-, and 20-year cutting cycles, commercial clearcutting (also called unregulated harvesting), fixed and modified (also called flexible) diameter-limit cutting, uniform shelterwood with two- and three-stage overstory removals (the three-stage shelterwood was later subdivided into four stands, two of which were precommercially thinned) and an unmanaged reference. Treatments were staggered in time so that treatment intervals coincided with management objectives and not specific dates (Figure 3.2). Changes over time in species composition and basal area of trees ≥ 1.3 cm in the treatments used in the present study can be seen in Figures 3.3 and 3.4.

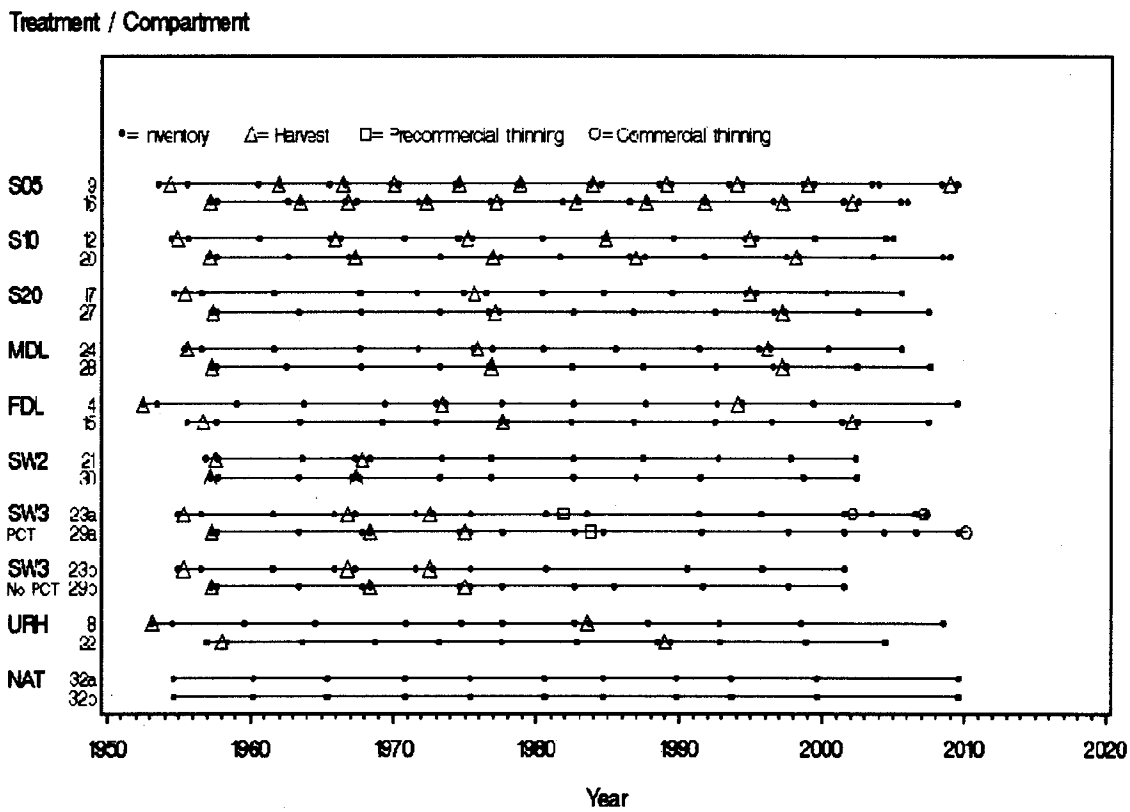

Figure 3.2. Treatment history on the PEF including inventories, harvests, pre-commercial and commercial thinning, courtesy of John Brissette, U.S. Forest Service.

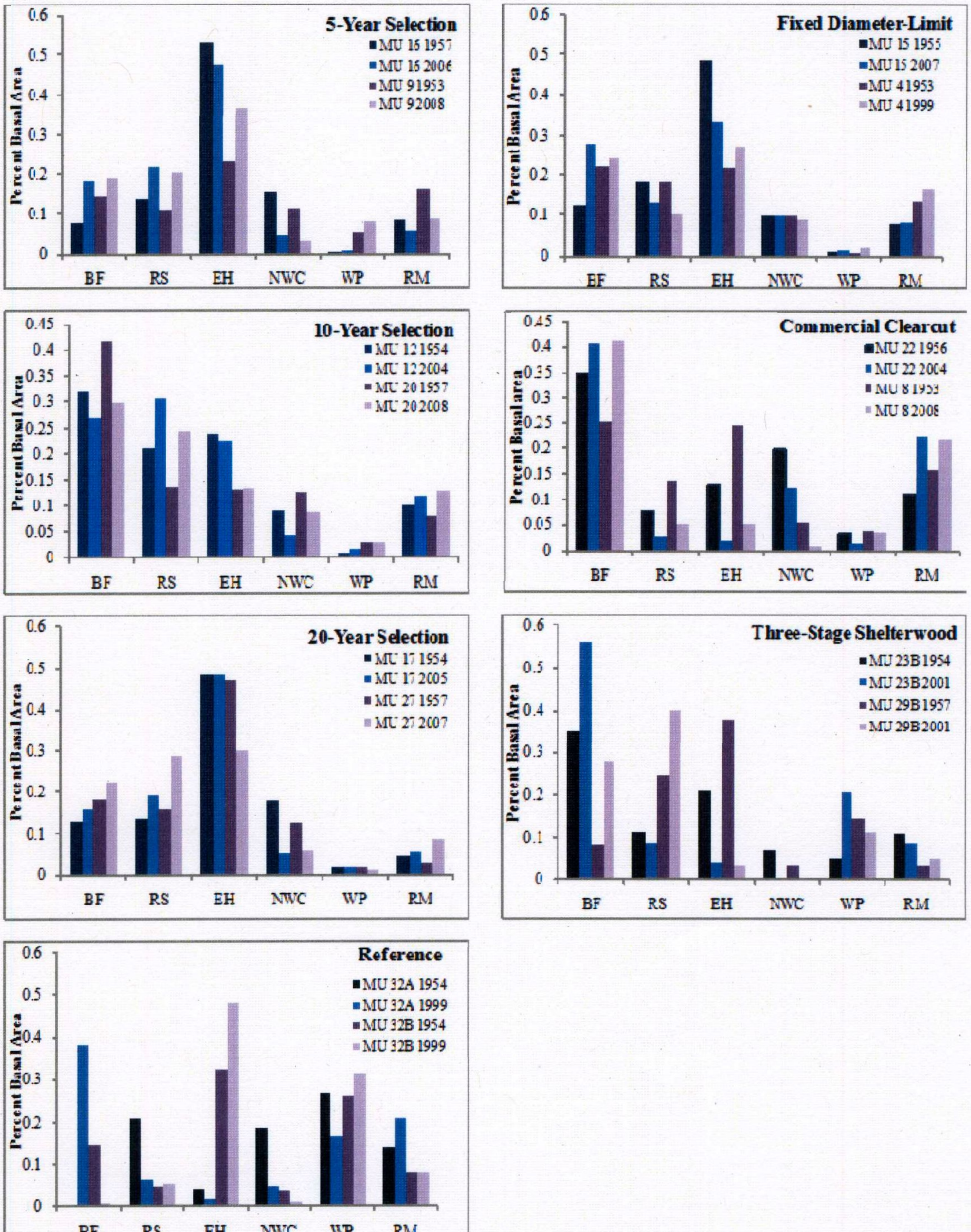

Figure 3.3. Percent basal area by species for the first and last inventory of each compartment. Species codes used in this graph are as follows: balsam fir (BF), red spruce (RS), eastern hemlock (EH), northern white-cedar (NWC), white pine (WP), and red maple (RM). Other species present in minor amounts are not shown.

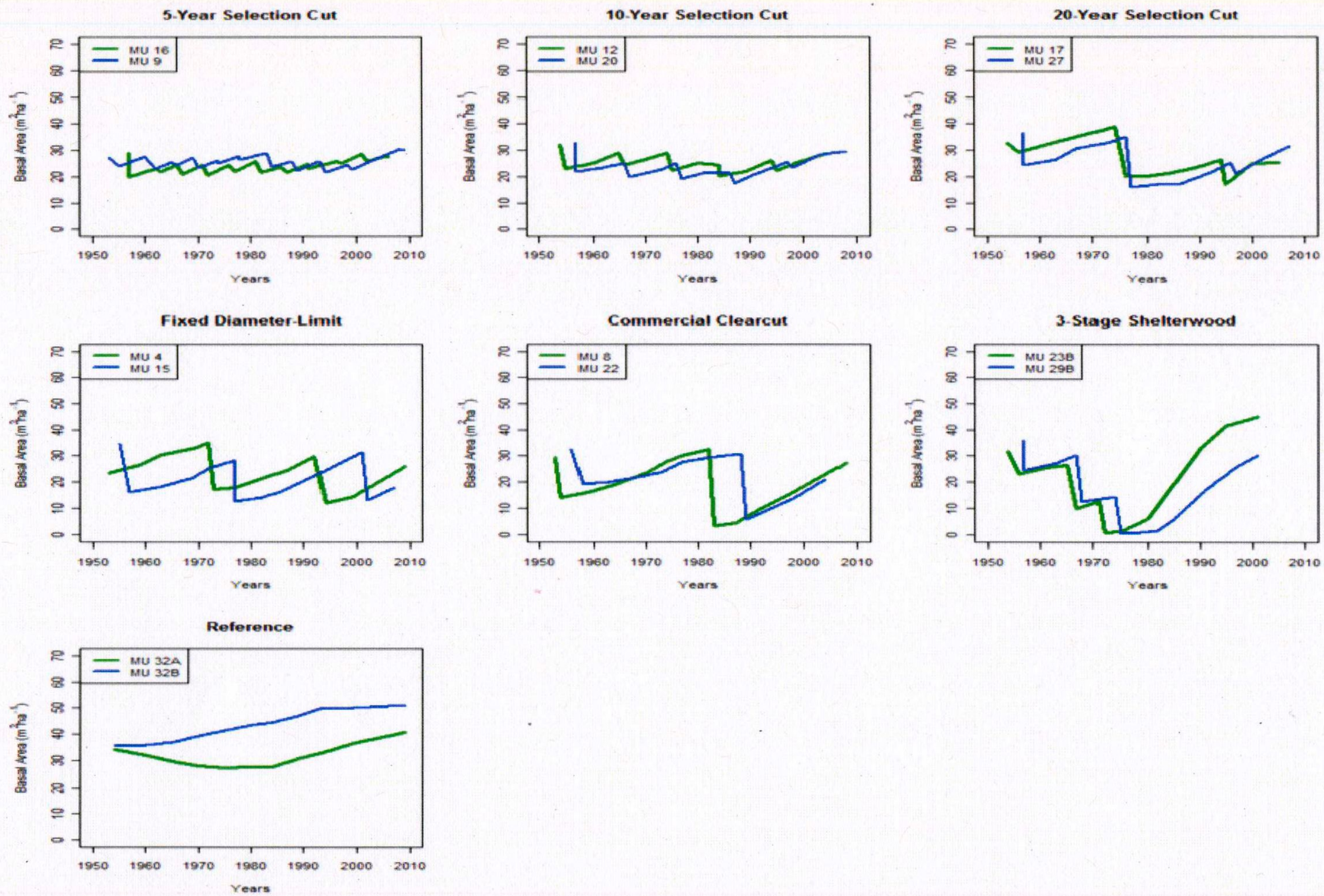

Figure 3.4. Graphs of BA (m^2 ha^{-1}) since treatment establishment on the Penobscot Experimental Forest. Data provided by the U.S. Forest Service.

Though the land for the PEF was bought by nine timberland owners in Maine and leased to the Forest Service for a commodity-production experiment, the study evolved to address the effects of silviculture and exploitive harvesting on stand dynamics and other forest concerns including productivity, resiliency and biological diversity (Sendak et al. 2003). When the experiment began, only basic mensurational data were collected, however over the past 60 years, research expanded to include leaf area and growth efficiency as well as course woody debris and regeneration, among other topics (for example, Kenefic and Seymour 1999; Seymour and Kenefic 2002; Weaver et al. 2009; Brissette et al. 2003; Kenefic et al. in press). Response variables measured on the long-term silvicultural study on the PEF currently include regeneration, species composition, tree and stand growth, productivity and quality (unpublished study plan, 2008).

The seven treatments measured for the current study are: no management (reference, UC), three-stage shelterwood (3SW), fixed diameter-limit cutting (FDL), commercial clearcutting (CC), and selection cutting on 5-, 10- and 20- year cutting cycles (S05, S10, and S20 respectively). All replicates of the treatments were measured, for a total of 14 compartments (stands) (Table 3.1). Diameter limits and BDq (basal area, maximum diameter and q factor [Meyer, 1952]) thresholds for the uneven-aged silviculture systems are found in Table 3.2. Compartments range in size from 2 to 17 ha. There are 8 to 21 nested 0.08-, 0.002-, and 0.008-ha Continuous Forest Inventory (CFI) plots in each compartment; these are inventoried every 5 or 10 years and before and after each treatment and provide a 15% sample of each stand. Prior to year 2000, saplings ≥ 1.3 cm DBH were measured on the nested 0.02-ha plot; beginning in year 2000 saplings were measured on nested 0.008-ha plots (Figure 3.5). Inventory data include species and

DBH for trees > 1.3 cm. Regeneration inventories began in the mid- 1960s, and include counts of seedlings by species and height classes (Table 3.3). There are three to four milacre regeneration plots around the perimeter of each 0.02-ha plot (Figure 3.5).

Table 3.1. Silvicultural treatments, compartments and treatment dates used for recruitment analysis on the Penobscot Experimental Forest in Bradley and Eddington, Maine.

Compartment	Treatment	Treatment Abbreviation	Treatment Description	Size (ha)	Treatment Dates
32A	Unmanaged Reference	UC	No management conducted after compartments were established. There had been unspecified partial cutting prior to 1900.	5.2	-
32B				2.2	
8	Commercial Clearcut	CC	Removal of all merchantable stems.	17.5	1953, 1983
22				13.7	1955, 1988
23B	3-Stage Shelterwood	3SW	Establishment cut followed by two overstory removal cuts.	5.0	1955, 1966, 1972
29B				3.0	1957, 1968, 1974
15	Fixed Diameter-Limit	FDL	Trees removed above specified diameters on variable cutting cycle. Harvests scheduled when volume achieves 147 m^3 per ha.	10.3	1956, 1971, 2001
4				10.1	1952, 1973, 1994
9	5-Year Selection Cutting	S05	Single-tree and small-group selection on a 5-year cutting cycle with periodic mechanical (brushsaw) release of selected saplings.	11.0	1954, 1961, 1966, 1970, 1974, 1978, 1983, 1989, 1993, 1998, 2003
16				6.6	1957, 1963, 1966, 1972, 1977, 1982, 1987, 1991, 1997, 2001, 2006
12	10-Year Selection Cutting	S10	Single-tree and small-group selection on a 10-year cutting cycle.	12.6	1954, 1965, 1975, 1984, 1994
20				8.6	1957, 1967, 1976, 1986, 1998
17	20-Year Selection Cutting	S20	Single-tree and small-group selection on a 20-year cutting cycle.	10.7	1955, 1975, 1994
27				8.2	1957, 1977, 1997

Table 3.2. Specific threshold levels for four treatments on the PEF from four study plans since experiment establishment. Note: q factors are expressed for 2.54-cm DBH classes, per the Forest Service study plan.

Treatment	Date of Study Plan[2]	Threshold Descriptions
Fixed Diameter-Limit	1953	Thresholds are 16.5 cm for balsam fir, 24.1 cm for spruce and hemlock, 26.7 cm for white pine, 19.1 cm for paper birch, and 16.5 cm for other hardwoods.
	1962	Thresholds are 16.5 cm for balsam fir, 24.1 cm for spruce and hemlock, 29.2 cm for white pine, 19.1 cm for cedar, 21.6 cm for paper birch, and 16.5 cm for other hardwoods.
	1974	Thresholds are 11.4 cm for balsam fir, 24.1 cm for spruce and hemlock, 26.7 cm for white pine, 19.1 cm for cedar, 19.1 cm for paper birch, and 11.4 cm for other hardwoods.
	2008	Thresholds are 14.0 cm for balsam fir, 24.1 cm for spruce and hemlock, 26.7 cm for white pine, 19.1 cm for cedar, 19.1 cm for paper birch, and 14.0 cm for other hardwoods.
5-Year Selection Cutting	1953	Structural goals are to retain 32.1-36.7 m^2/ha (trees > 1.3 cm), residual max diameter of 40.6 cm for pulpwood and 61 cm for multiple products, and q = 1.45 for pulpwood and 1.4 for multiple products.
	1962	Structural goals are to retain 27.5 m^2/ha (trees > 1.3 cm), residual max diameter of 40.6 cm for pulpwood and 61 cm for multiple products, and q = 1.4 for pulp and 1.3 for multiple products.
	1974	Structural goals are to retain 26.4 m^2/ha (trees > 1.3 cm), residual max diameter of 50.8 cm, and q = 1.4.
	2008	Structural goal is to retain 24.1 m^2/ha (trees > 11.4 cm). Residual max diameter and q factor vary by species group.
10-Year Selection Cutting	1953	Structural goals are to retain 32.1 - 36.7 m^2/ha, residual max diameter of 40.6 cm for pulp and 61 cm for multiple product, and q = 1.45 for pulp and 1.4 for multiple product.
	1962	Structural goals are to retain 24.1 m^2/ha (trees > 1.3 cm), residual max diameter of 40.6 cm for pulp and 61 cm for multiple product, and q = 1.4 for pulp and 1.3 for multiple products.
	1974	Structural goals are to retain 23.0 m^2/ha (trees > 1.3 cm), residual max diameter of 50.8 cm, and q = 1.4.
	2008	Structural goal is to retain 20.7 m^2/ha (trees > 11.4 cm). Residual max diameter and q factor vary by species group.
20-Year Selection Cutting	1953	Structural goals are to retain 25.3 - 29.8 m^2/ha, residual max diameter of 40.6 cm for pulp and 61 cm for multiple product, and q = 1.45 for pulp and 1.4 for multiple products.
	1962	Structural goals are to retain 18.4 m^2/ha (trees > 1.3 cm), residual max diameter of 40.6 cm for pulp and 61 cm for multiple product, and q = 1.4 for pulp and 1.3 for multiple products.
	1974	Structural goals are to retain 18.4 m^2/ha (trees > 1.3 cm), residual max diameter of 50.8 cm, and q = 1.4.
	2008	Structural goal is to retain 16.1 m^2/ha (trees > 11.4 cm). Residual max diameter and q factor vary by species group.

[2] Study plans in 1953 and 1962 were written by T.F. McLintock. The 1974 study plan was written by Robert M. Frank, Jr. and the 2008 study plan was written by John C. Brissette and Laura S. Kenefic.

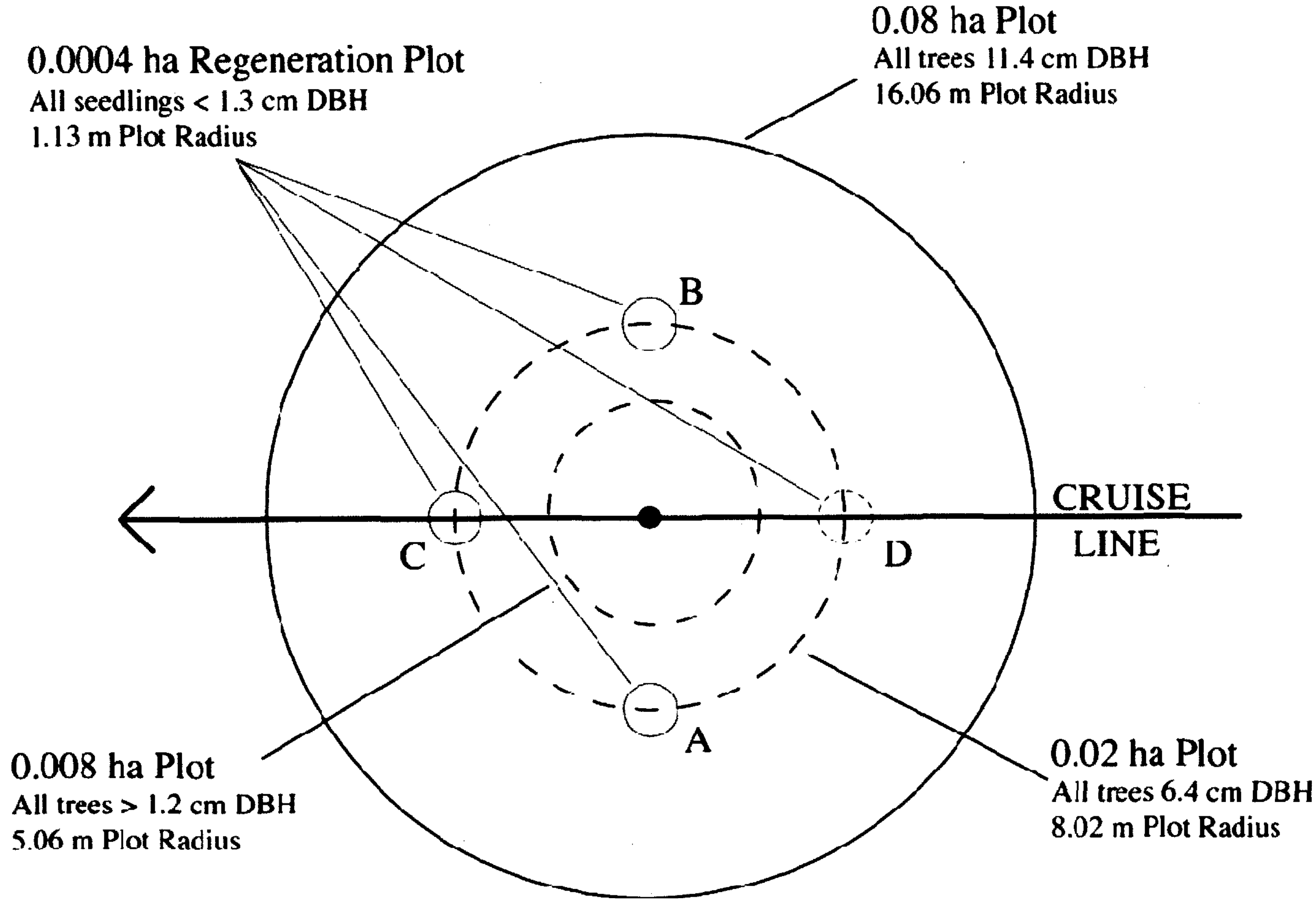

Figure 3.5. CFI plot design used on the PEF field season 2000 and after. Seedlings measured for mammalian herbivory on the 3-4 milacre regeneration plots located around the rim of the 0.02 ha plot. Milacre plot D only found in the unharvested control compartments (32A and 32B).

DATA COLLECTION

Each of the plots in the treatments described above was measured during the summer of 2010. In all compartments, with exception of the reference (32A and 32B), CFI plots contained three 1.13-m radius regeneration plots. The reference contained four regeneration plots (Figure 3.2). Browsing was measured by counting and recording each seedling by species, height class (Table 3.3) and whether or not it was browsed. If the seedling was browsed, the percentage of tissue missing was tallied using the following scale: 1-24%, 25-49%, 50-74%, 74-99% and 100% (1-5 respectively). Finally, animal group classification was established as follows: (1) deer or moose and (2) hare or rodent. Grouping was conducted like this because moose and deer tend to rip vegetation when browsing, while hare and rodents cleanly break lateral and meristematic tissue. This is because deer lack incisors in their upper front jaw, whereas hare and other rodents have teeth that cut through twigs and branches like a knife.

Table 3.3. Height classes of seedlings on regeneration plots of the PEF.

Class	Height
1	< 15.2 cm
2	15.2 cm – 30.5 cm
3	0.31 m – 0.61 m
4	0.62 m – 1.37 m
5	1.38 m – 1.2 cm dbh

STATISTICAL ANALYSIS

Tree-level

Probability of browsing, or the likelihood of a seedling being browsed, was assessed using multiple logistic regression, while species and treatment pairwise comparisons were obtained using Tukey's HSD and $\alpha = 0.05$. This was done using a generalized linear mixed model (GLMM) for binomial data using the SAS statistical program (SAS Institute Inc. 2008); the dependent variable was browsed or not (1 or 0) using species group (Table 3.4), silvicultural treatment, and height class as independent variables. Random effects included compartment and plot within compartment. Individual species were incorporated into the model as the dependent variable where $n > 40$ observations. Species included were red spruce, balsam fir, white pine, eastern hemlock, northern white-cedar and red maple (black ash (*Fraxinus nigra*) had $n > 40$, but was removed from the analysis due to few, spatially concentrated observations). Statistical significance was deemed at $\alpha = 0.05$. Multiple pairwise comparisons using Tukey's adjustment was used to evaluate within factor differences. Intolerant softwoods were removed from this analysis due to small numbers of observations ($n < 5$).

Table 3.4. Species associated with each of the six species groups (Burns and Honkala 1990). Tolerance reference is ability to withstand shade.

Species Group	Species Associated
ISW	Tamarack (*Larix laricina*); Red pine (*Pinus resinosa*)
TSW	Balsam fir; Spruce spp.; Eastern hemlock; Northern white-cedar
INTSW	Eastern white pine
IHW	Paper birch; Gray birch (*Betula populifolia*); Trembling aspen; Bigtooth aspen; Black cherry (*Prunus serotina*); Balsam poplar (*Populus balsamifera*); Pin cherry (*Prunus pensylvanica*)
THW	Sugar maple; American beech; Eastern hophornbeam (*Ostrya virginiana*); American basswood (*Tilia americana*); Striped maple (*Acer pensylvaticum*); Mountain maple (*Acer spicatum*)
INTHW	White ash (*Fraxinus americana*); black ash; Yellow birch (*Betula alleghaniensis*); Red maple; Northern red oak (*Quercus rubra*)

The R statistical program (R Development Core Team 2008) and the lme4 and nlme libraries linear mixed effects model (lmer) were used to assess damage class (amount of foliage and tissue removed from a seedling, Table 3.5). The number of seedlings in each damage class for a given species, treatment and plot was used as a discrete dependent variable. Independent variables for the model were species, height class, treatment and animal. Species used in the model were those used in the probability model. Random effects were compartment and plot within compartment. Statistical significance was set at $\alpha = 0.05$. Multiple pairwise comparisons using Tukey's adjustment were used to evaluate within factor differences.

Table 3.5. Damage classes according to percentage of foliage removed from seedlings due to browsing.

Damage Class	Percentage of Foliage Removed due to Browsing
1	< 25%
2	26% - 50%
3	51% - 75%
4	76% - 99%
5	100%

Plot-level

Using the R statistical program (R Development Core Team 2008) and the lme4 and nlme libraries, a linear mixed effects model was used to assess severity: proportion of seedlings browsed at the plot level. The logit transformation of average severity by plot was used as a dependent variable to account for it being a proportion. The independent variable was treatment. Multiple pairwise comparisons using Tukey's adjustment were used to evaluate within-treatment differences.

Results

TREE-LEVEL

Probability of Browsing

Browsing probability was found to be a function of height class and tolerance group ($p < 0.05$) (Tables 3.6 and 3.7). Treatment was not a significant predictor of probability of browsing. No statistically significant interactions between factors were detected.

Table 3.6. Fixed effects, standard errors and p-values for the browsing model (Probability of browsing). Pairwise comparisons using Tukey's adjustment show inter-factor differences at $\alpha = 0.05$. HtClass5, TSW, and UC are the reference levels.

Fixed Effects	Estimate	Error	DF	t Value	Pr > |t|	Pairwise
Intercept	-3.0540	0.6156	7	-4.96	0.0016	B
HtClass 1	-2.0370	0.2017	5732	-10.10	<0.0001	C
HtClass 2	0.6025	0.1900	5732	3.17	0.0015	A
HtClass 3	0.8340	0.2047	5732	4.07	<0.0001	A
HtClass 4	0.5916	0.2074	5732	2.85	0.0043	A
IHW	2.4730	0.3625	5732	6.82	<0.0001	AD
IntHW	1.0429	0.1269	5732	8.22	<0.0001	B
IntSW	0.7882	0.5396	5732	1.46	0.1441	BCD
THW	4.0556	0.5716	5732	7.10	<0.0001	A
TSW						C
3SW	0.9826	0.8536	5732	1.15	0.2497	A
CC	1.3220	0.8151	5732	1.62	0.1049	A
FDL	0.8613	0.8243	5732	1.04	0.2962	A
S05	1.2289	0.8150	5732	1.51	0.1317	A
S10	1.2891	0.8150	5732	1.58	0.1138	A
S20	0.1823	0.8317	5732	0.22	0.8265	A
UC						A

Table 3.7. Fixed effects summary

Effects	DF	F Value	Pr > F
HtClass	4	114.30	< 0.0001
Grouped	5	27.24	< 0.0001
Trt	6	0.87	0.5191

Pairwise comparisons (Figure 3.6) of probability of browsing using Tukey's HSD showed that THW and IHWs, which had the highest probabilities of browsing at 86% and 56%, respectively, were not different from one another at $\alpha = 0.05$. IntHWs (24%) and IntSWs (19%), as well as IntSWs and TSWs (10%), were also undifferentiated from one another. IntSWs were not statistically different from IHWs. TSW, which had the lowest probability of browsing, were statistically different from all hardwood groups.

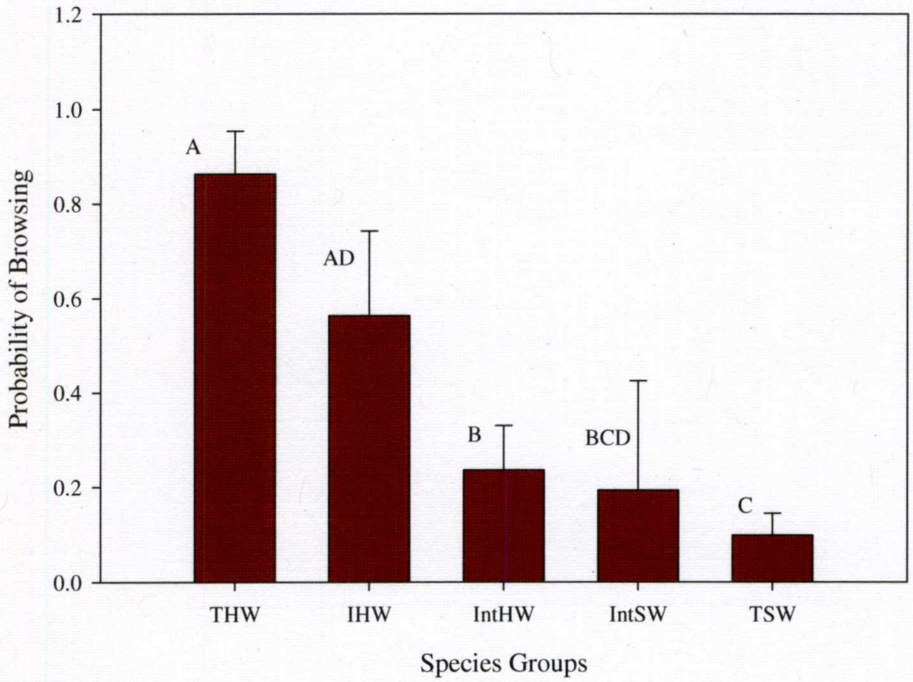

Figure 3.6. Least squares means for probability of browsing for five tolerance groups on the PEF. Letters indicate pairwise comparisons and statistical differences between species groups at $\alpha = 0.05$.

When the 6 species of interest on the PEF were analyzed individually rather than using tolerance group (Table 3.8; Figure 3.7), red spruce (42%), northern white-cedar (39%) and white pine (19%) were not significantly different from one another, nor were eastern hemlock (8%) and balsam fir (5%). White pine and red maple (19%) were also not significantly different from one another. Red spruce, northern white-cedar and red maple had higher browsing probabilities than eastern hemlock and balsam fir.

Table 3.8. Statistical summary table and pairwise comparisons of six species of interest on the PEF. Tukey's adjustment was used to compare species to one another.

Species	Estimate	Error	z-value	P-value	Pairwise
Red Spruce	2.6266	0.1779	14.764	<2e-16	A
N White-Cedar	2.5024	0.2439	10.261	<2e-16	A
E White Pine	1.5093	0.5302	2.794	0.0052	ABC
Red Maple	1.5055	0.1674	8.992	<2e-16	B
Eastern Hemlock	0.4471	0.1957	2.284	0.0224	C
Balsam Fir	-4.5528	0.5302	-8.587	<2e-16	C

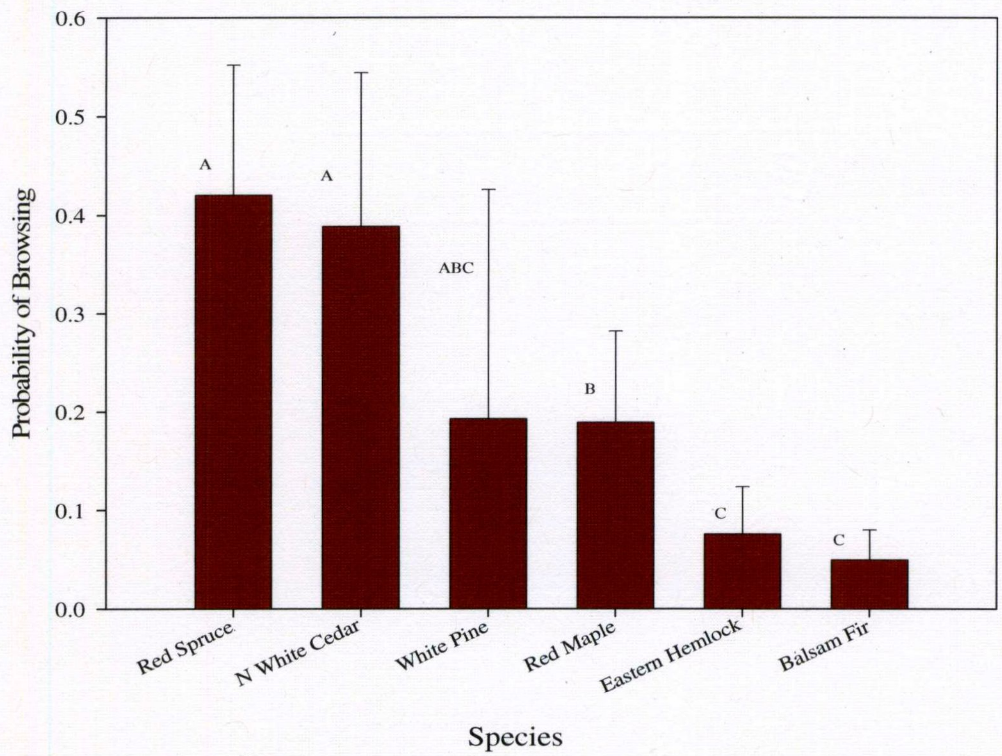

Figure 3.7. Least squares means for probability of being browsed and upper confidence limits for six selected species on the PEF. Letters indicate pairwise comparisons and statistical differences between species at $\alpha = 0.05$.

Probability of browsing for seedlings in height classes 1-3 (61%, 55%, and 55% respectively) did not differ from each other, but these classes were statistically different from height classes 4 and 5 (40% and 8% respectively). Height classes 4 and 5 were also statistically different from one another. Probability of browsing was found to be highest in height classes 1-3 and lowest in height class 5 (Figure 3.8).

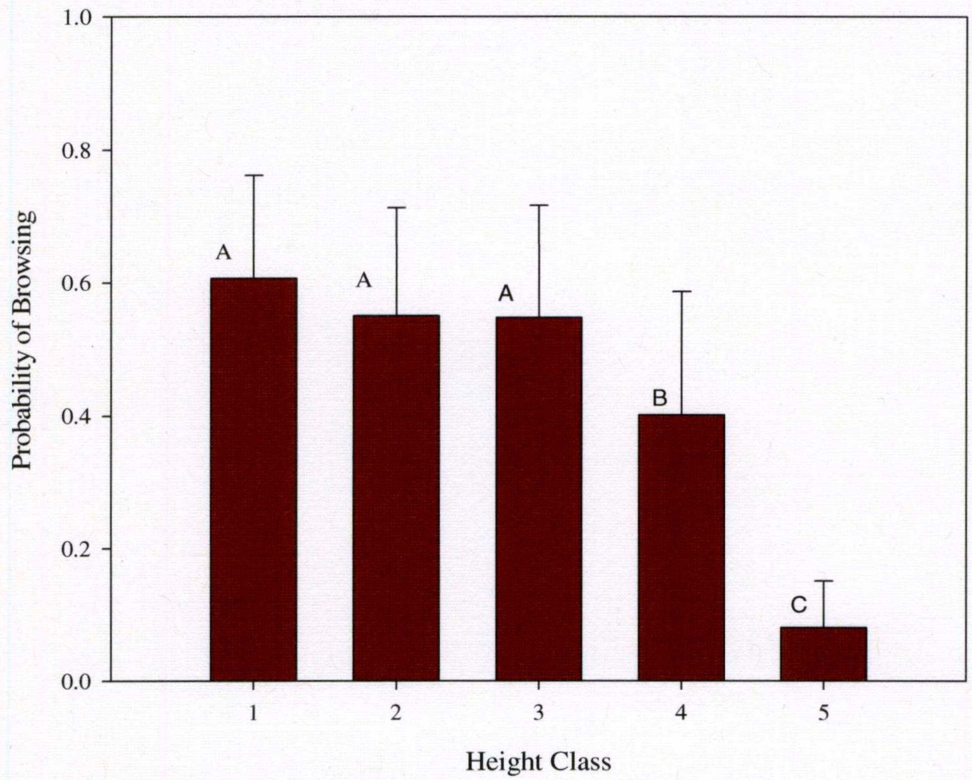

Figure 3.8. Least squares means for probability of browsing and upper confidence limits for five height classes of regeneration on the PEF. Letters indicate pairwise comparisons and statistical differences among height classes at $\alpha = 0.05$.

Browsing Damage

Browsing damage, the amount of foliage and tissue removed from individual seedlings, was assessed and given a number code of one through five, with five being the most severe (Table 3.5). These codes were then used to assess the damage by treatment, species, height class and animal group (deer/moose and hare/rodent).There was no statistical significance found for any of the factors used in the browsing damage model.

Tree-level variability in browsing damage for each of the factors evaluated can be seen in Figures 3.9 to 3.12. The largest amount of variation in browsing damage was observed in the CC, S10, and S20, though most damage was between classes 1 and 3. Damage class means generally fall around class 2 with the exception of the FDL, which has a mean of 3 and the 3SW with a mean of 1. Within-species variation in damage was greatest in red spruce, red maple, and northern white-cedar. Damage class means range from 1 in eastern white pine to 3 in red maple. Damage class means for all height classes were class 2, though variability in damage was greatest in height classes 1, 2, and 4. With regard to animal groups, deer/moose resulted in a higher damage class mean of 2.5, whereas hare/rodent resulted in a mean damage class of 2.

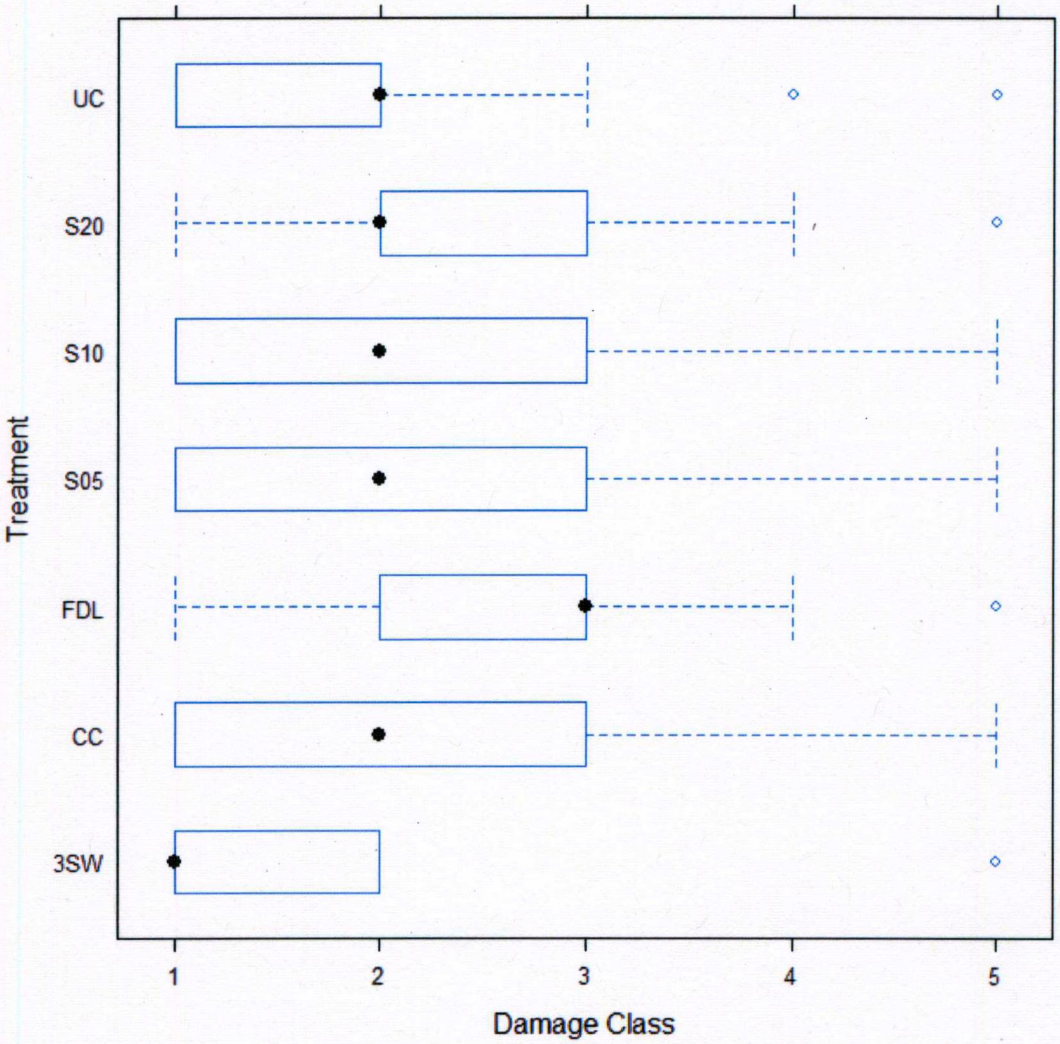

Figure 3.9. Means and ranges of damage found for each of the seven treatments on the PEF.

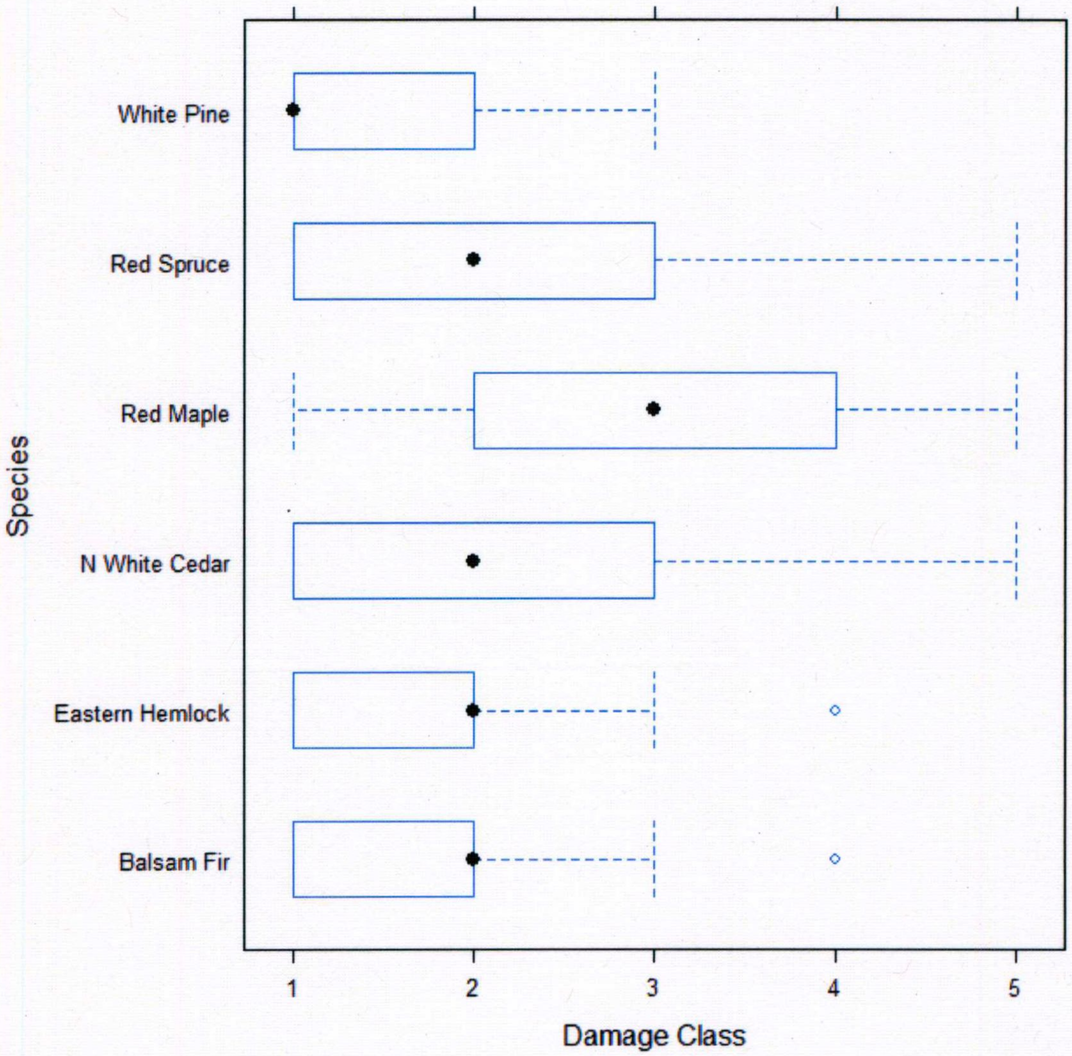

Figure 3.10. Means and ranges of damage found for six selected species on the PEF.

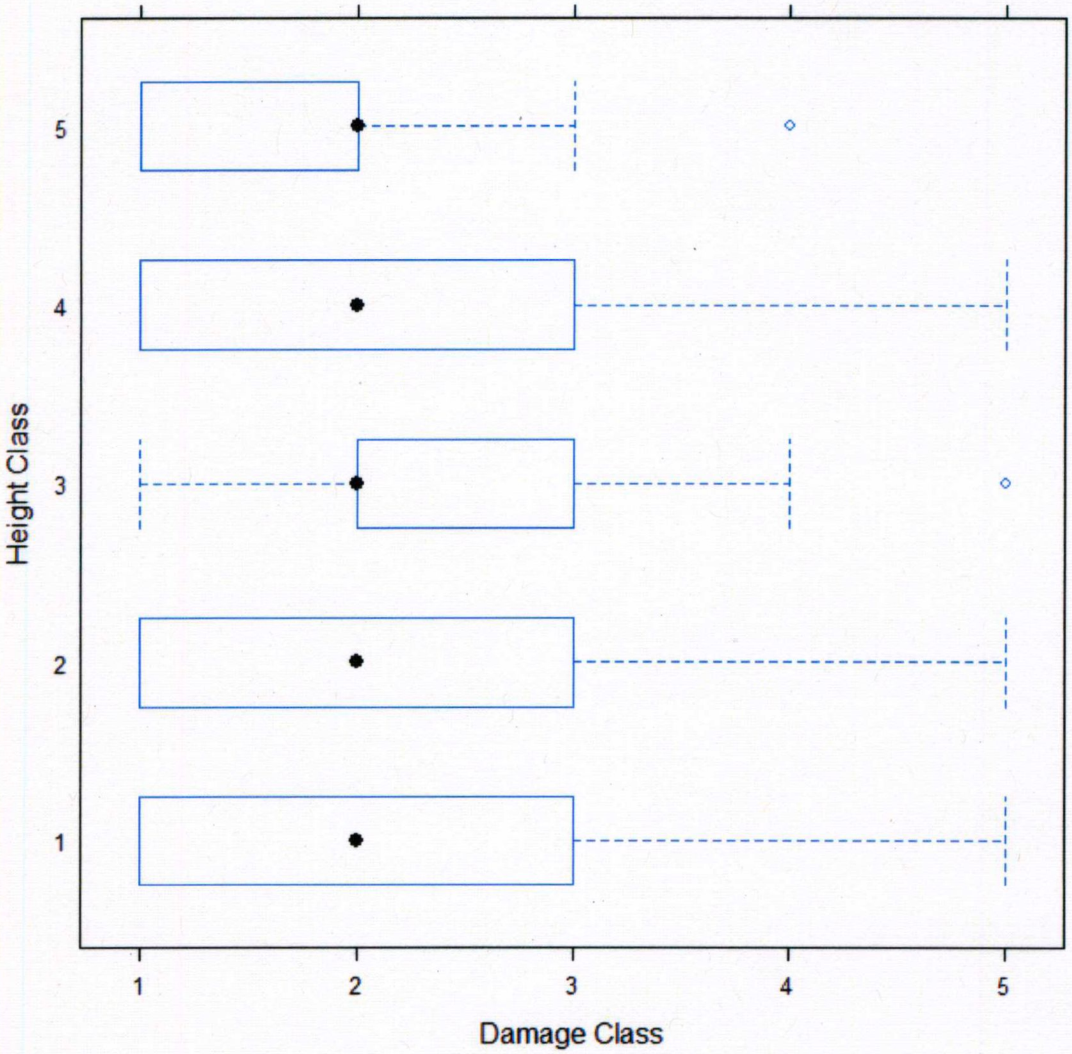

Figure 3.11. Means and ranges of damage for five seedling height classes on the PEF.

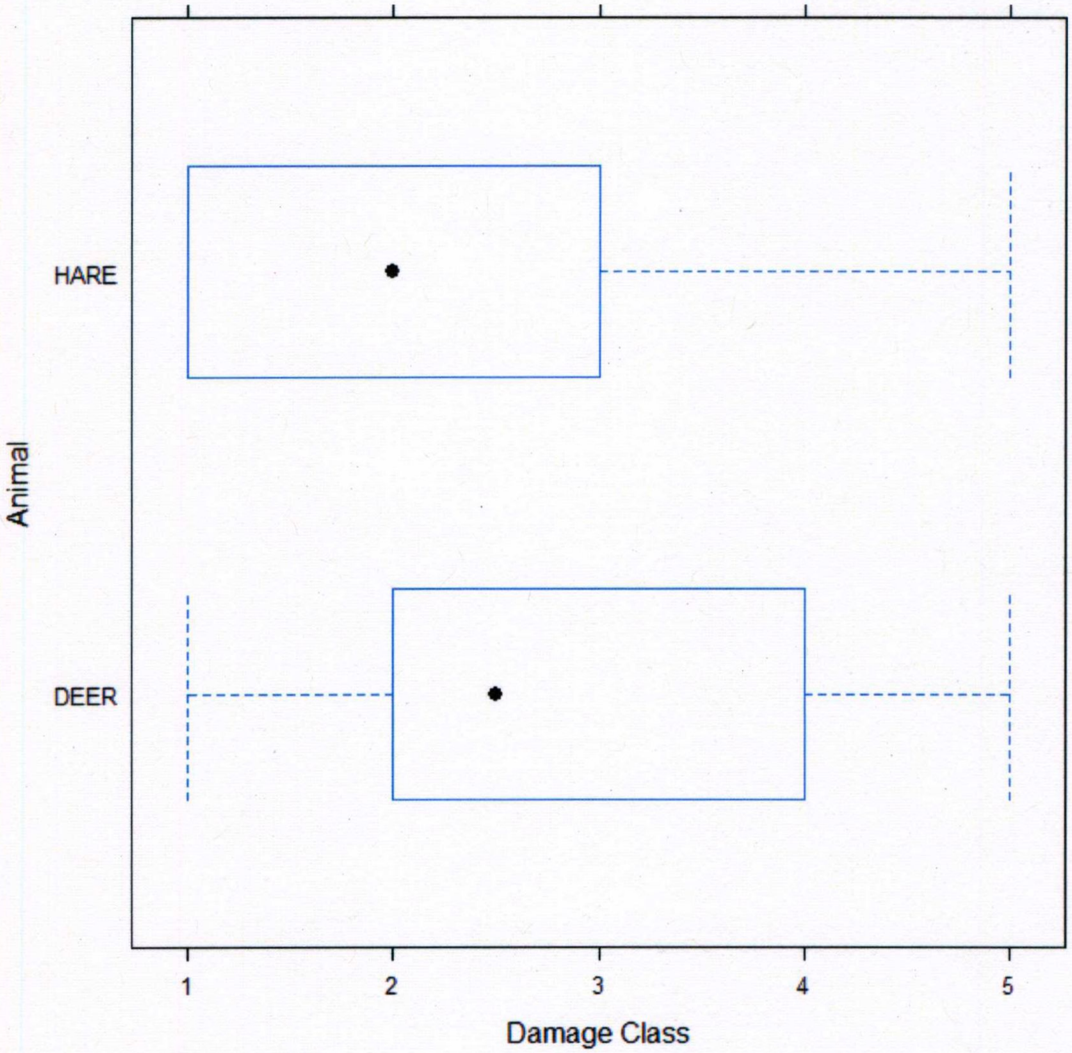

Figure 3.12. Means and ranges of damage for two animal groups (hare/rodent and deer/moose) on the PEF.

PLOT-LEVEL

Browsing Severity

None of the factors used in this analysis (treatment, species, height class or animal group) were statistically related to browsing severity. Greatest variation in browsing severity is found in the 3SW and FDL treatments, which each range from about 0% to 40% browsed of seedlings browsed (Figure 3.13). In general, severity means fall around 10% across all treatments. Browsing severity means were highest in the S05 and S10 and CC compartments (Table 3.10). An inverse distance weighted map of plot level browsing severities on the PEF can be seen in Figure 3.14.

Browsing severities across species may be seen in Table 3.9. Severity remains high across all hardwood species, except red maple (6.3%), ranging from 24.4% to 100%. Softwoods range from 0% in white spruce to 37.4% in red spruce. Overall, browsing severity on the PEF, independent of species, is lowest in height class 1 at approximately 3.5%. Height classes 2 and 3 showed the highest browse severity at 26.5% and 26.0% respectively, followed by height class 4 at 19.9% and height class 5 at 15.9%.

Table 3.9. Browsing severity by species; species of interest are in bold.

	Browsed			
Species	**No**	**Yes**	**n**	**Severity**
American Beech	4	2	6	33.3%
Black Ash	53	17	70	24.3%
Black Cherry	0	6	6	100.0%
Balsam Fir	**1827**	**89**	**1916**	**4.6%**
Basswood	1	11	12	91.7%
Eastern Hemlock	**773**	**61**	**834**	**7.3%**
Gray Birch	6	5	11	45.5%
Ironwood	0	1	1	100.0%
Mountain Maple	0	1	1	100.0%
N White Cedar	**142**	**46**	**188**	**24.5%**
Paper Birch	18	9	27	33.3%
Pin Cherry	3	5	8	62.5%
Red Maple	**2032**	**136**	**2168**	**6.3%**
Red Oak	6	5	11	45.5%
Red Pine	0	1	1	100.0%
Red Spruce	**243**	**145**	**388**	**37.4%**
Sugar Maple	0	2	2	100.0%
Tamarack	1	0	1	0.0%
White Ash	5	20	25	80.0%
White Pine	**41**	**5**	**46**	**10.9%**
White Spruce	2	0	2	0.0%
Yellow Birch	6	25	31	80.6%

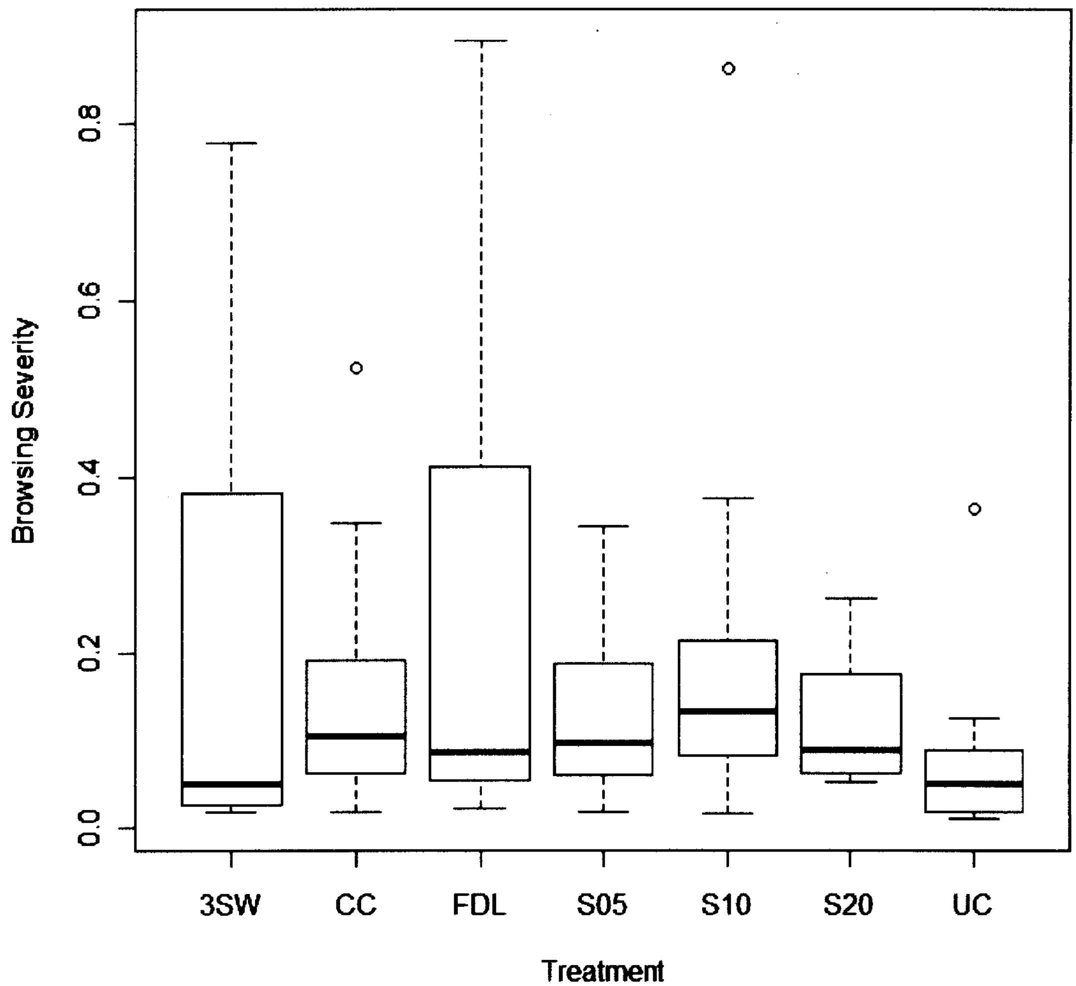

Figure 3.13. Means and ranges of plot-level browsing severity across treatments on the PEF.

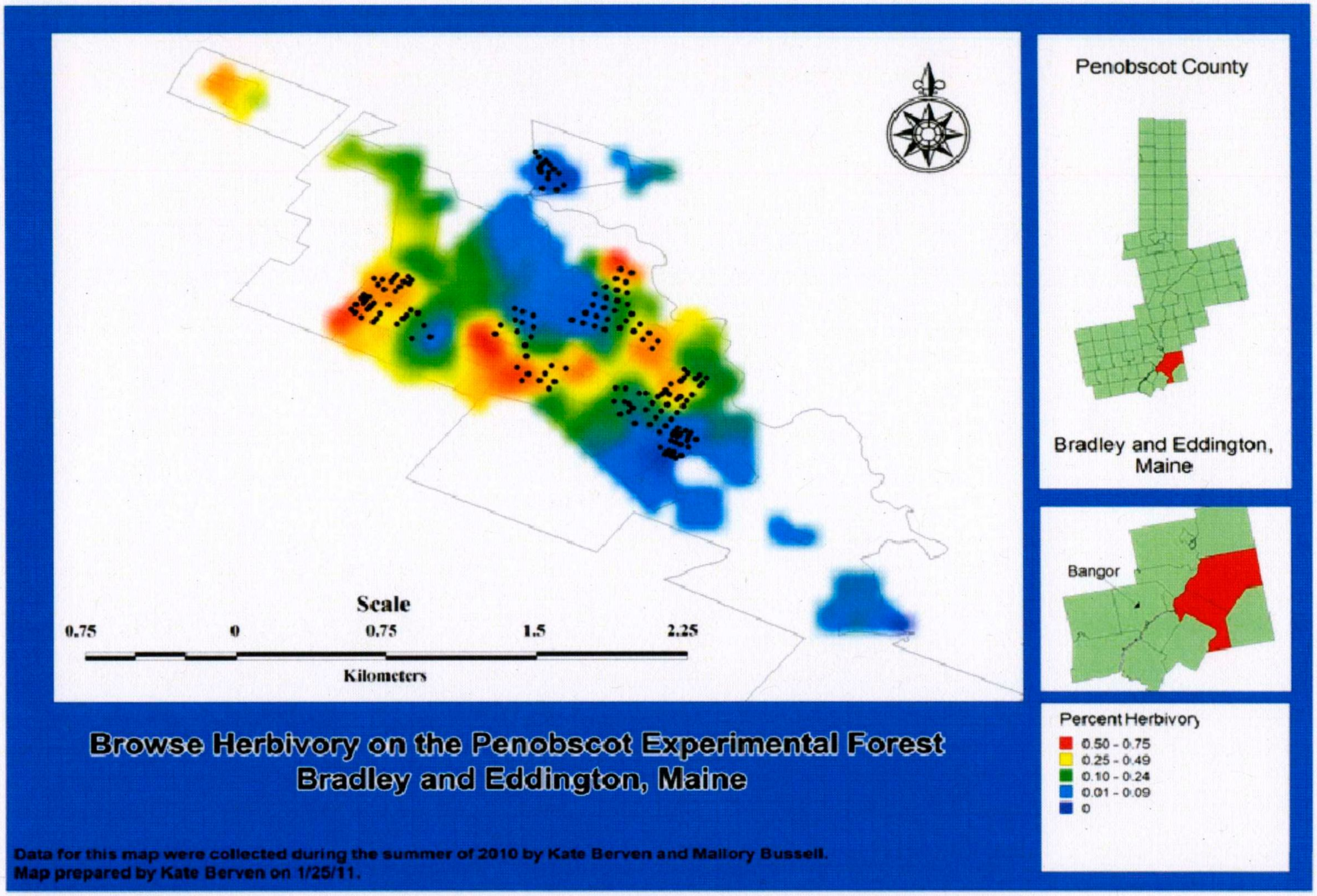

Figure 3.14. Plot-level browsing severity on the PEF calculated by inverse distance weighed interpolation; black dots represent sample points.

Raw data of browsing severity by species and height classes may be seen in Figure 3.15. White pine and northern white-cedar are not represented in the larger height classes. Red maple had the highest overall severity (53%, 81%, 72% and 91% in classes 2-4 respectively), except height class 1 (2%). Balsam fir and eastern hemlock both have low severities across all height classes: 1% to 13%. Red spruce had very little variation in browsing severity (23%, 53%, 46%, 40%, and 21%) for height classes 1-5, respectively.

Table 3.10. Average browsing severity by treatment and range of severity across replicated treatments.

	Average	**Range**	
Treatment	**Browsing Severity (%)**	**Min**	**Max**
3SW	6.3	4.6	8
CC	13.4	11.2	15.7
FDL	10.1	5.9	14.4
S05	12.4	8.1	16.7
S10	13.6	11.6	15.6
S20	7.7	2.1	13.4
UC	5.0	1.7	8.3

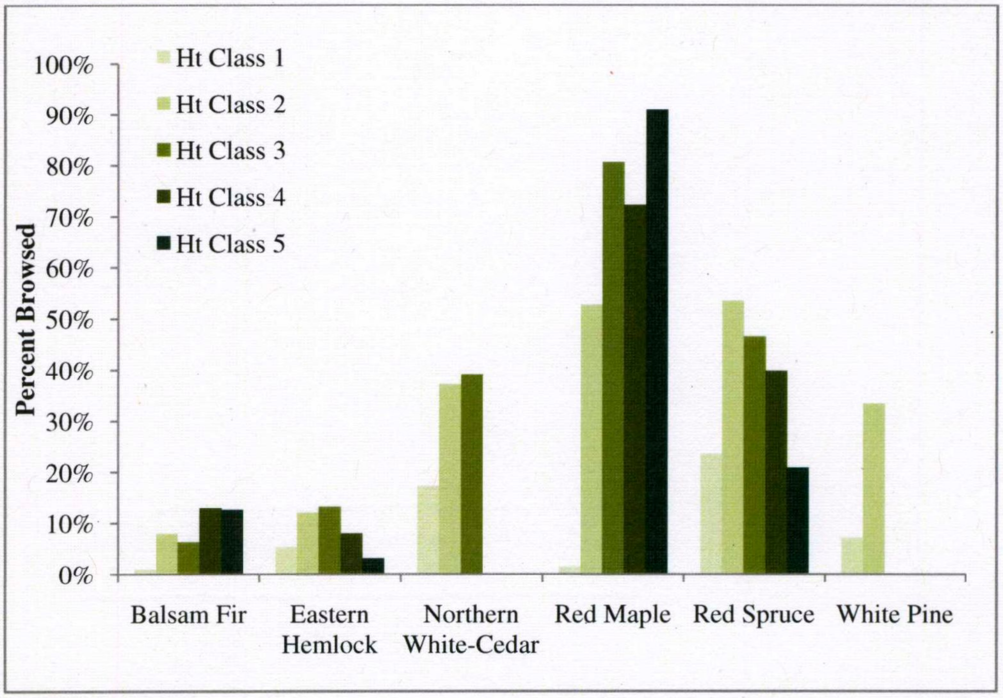

Figure 3.15. Browsing severity of six selected Acadian Forest species across five height classes. Northern white-cedar not represented in height classes 4 and 5. White pine was not represented in height class 5. White pine in height classes 3 and 4 had 0% browsing severity.

Discussion

TREE-LEVEL

Browsing on the PEF is a factor that is likely to hinder the ability of certain tree species to recruit into larger size classes. Seedling height is a factor which influences a seedling's probability of being browsed. Probability of browsing generally decreased with increasing height, though these data are somewhat misleading for the smallest class. Height class 1 was classified as any seedling <6", however a large number of red maple and balsam fir germinants (1,996 and 1,096 respectively) may have skewed the data, causing browsing severity and predicted values to be lower than if only seedlings from the previous year and older been measured. Although age was not measured, there were a high number of first year germinants, which could be distinguished from older seedlings.

Northern white-cedar is a favored browse species for white-tailed deer and has lower sapling recruitment rates than other species on the PEF despite seedling establishment across all treatments (Larouche et al. 2010). The absence of cedar in larger height classes indicates that there are factors inhibiting its growth. It is likely that high browsing of the lower height classes is preventing seedlings from reaching larger classes. Of the 32% of northern white-cedar seedlings browsed on the PEF, 53% were accounted for by deer/moose; the remaining 47% were browsed by hare/rodents. Repercussions of reduced recruitment could lead to diminished populations of northern white-cedar in the larger diameter classes. Aldous (1941) found that northern white-cedar will not survive repeated browsing if more than 25% of the foliage is removed annually, while Cornett et al. (2000) found that greater than 75% of unfenced cedar seedlings were browsed within three years, indicating a shift in forest composition to hardwoods. A controlled experiment using exclosures to prevent browsing of northern white-cedar from deer, hare and rodents found that browsing was eliminated until height growth exceeded exclosure height (Davis et al. 1998).

Among the species of interest on the PEF, northern white-cedar and red spruce are the most likely browsed, leading to damage inhibiting recruitment. Evidence suggests that northern white-cedar has been in decline across the region since 1995 (McWillams et al. 2005), which is seen as a lack of recruitment in comparison to harvest levels (Hofmeyer et al. 2009). Due to the slow-growing nature of the species, heavy browsing impedes the species' ability to gain height growth and may be a decisive factor leading to a lack of recruitment across the PEF and other regions of Maine.

Red spruce is a species that managers struggle to ensure is recruited into the larger diameter classes because it tends to be less vigorous in terms of basal area growth than its competitors (Hofmeyer et al. 2006). Furthermore, there is no light level which favors spruce in the understory over its tolerant conifer competitors (Moores et al. 2007). Its primary competitor, balsam fir, reproduces more vigorously and is more advantageous in the seedling state (Weaver 2009). Because red spruce may remain in the understory for many years before becoming released (Seymour 1992), it is also more prone to prolonged browsing damage. There is little evidence from the literature suggesting that red spruce is a favored browse species by any animal; however, this study shows that snowshoe hare or rodents may have more of an impact on red spruce than otherwise thought. As a slow-growing, tolerant species, red spruce seedlings are in danger of having another recruitment limitation.

Although treatment had no effect on probability of browsing, the intensity of silvicultural regimes affects browse availability and the tree species regenerated. Four of the six species of interest outlined in this chapter (balsam fir, eastern white pine, northern white-cedar, and red maple) are preferred winter browse for deer (Banasiak 1961) and moose (Lautenschlager 1985). In general, however, hardwood species tend to have higher browsing severity. Uneven-aged management, i.e. selection cutting on the PEF, aims to create stands of high-value trees, while removing mature trees, tending immature classes and creating regeneration over the long-term (Kenefic et al. 2005). These treatments tend to favor the height growth of shade-tolerant conifers, which are responsive to increases in canopy openness in shaded conditions (Moores et al. 2007). Of the herbivores discussed in this study, all tend to favor early successional forests created by clearcutting or partial gap harvesting, which creates ample edge and hardwood regeneration (Monthey 1984; Waller and Alverson 1997; Jakubus 2002). In general, there were no treatment effects for probability of browsing on the PEF. Where browsing does become problematic in the Acadian Forest, selection cutting may favor tolerant conifers, while reducing the amount of browse preferred by herbivores of the region.

PLOT-LEVEL

Red spruce is a common species to the Acadian, mixed northern conifer forests of Maine. High browsing severity of red spruce on the PEF is almost completely accounted for by hare/rodents. Of the 37% of red spruce seedlings browsed, 95% were browsed by hare/rodents and 5% were browsed by deer/moose. This suggests that in addition to other complications impeding recruitment into larger size classes, hare/rodents may be a factor limiting recruitment of red spruce.

Eastern hemlock appeared to have little browsing pressure in this study, however browsing severities in the 3SW and CC were relatively high (23.3% and 16.7% respectively), indicating that these areas may not provide preferred browse. Alverson et al. (1988) and others found hemlock regeneration failures due to browsing by deer, even in favorable habitats and stand conditions (Lorimer 1996). Areas with high deer populations rarely have seedlings greater than 1.3 cm dbh without browsing damage (Swift 1948; Lorimer 1996). Furthermore, snowshoe hare also browse on eastern hemlock regeneration (Swift 1948; Sage 1986). Goerlich and Nyland (2000) maintain that eastern hemlock requires a number of factors including suitable seed, moisture, partial shade and freedom from prolonged browsing in order to have successful seedling development.

White-tailed deer are abundant throughout the region. The MDIFW estimate deer wintering populations to be 255,000 individuals in central Maine. This is near the estimated population high of 275,000 achieved in the late 1950s. Current goals to increase populations to 270,000-330,000 by increasing deer wintering habitat as well as coyote population reductions have been set (MDIFW). Because forest composition and structural changes due to browsing are often subtle and slow to develop (Waller and Alverson 1997), increased deer populations may have unforeseen effects on forest composition as well as indirect effects which reach to all levels of the forest ecosystem.

Conclusion

Herbivory has a great impact on seedling development and longevity. In Maine, there are many mammals which use woody browse for nutrition and survival. Deer, moose, hare, and rodents are present and active browsers across the Acadian Forest and the PEF (Blum 1977; Larouche 2010). Deer alone have long been known to adversely affect the absolute and relative abundance of woody species (Leopold et al. 1947; Webb et al. 1956; Waller and Alverson 1997). In some regions, deer have more effect on tree longevity and mortality than environmental and climatic factors (Boerner and Brinkman 1996).

Browsing should be considered in management plans of the Acadian Forest. Although treatment was not a determinant of probability or severity of browsing, mammals and other herbivores have tree species preferences. Two essential species of the region, red spruce and northern white-cedar, are at risk of being reduced in the forest. These two species should be favored in management plans to increase chances of recruitment. Red spruce (Weaver 2007) and northern white-cedar (Johnston 1990) are ecologically important, and critical to Maine's lumber market. Because herbivores have direct and indirect effects on forest dynamics which are often hard to interpret, long-term research projects should be set in place to determine forest response to browsing in the Acadian Forests of Maine. Larger height classes had lower probabilities of browsing. Accelerating growth on saplings by releasing them from overstory competition may reduce browsing on slower-growing species such as red spruce and northern white-cedar.

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APPENDIX A: PARTIAL ANNOTATED BIBLIOGRAPHY

Introduction

Long-term research is critical to our understanding of forest dynamics. Observations made over decades or centuries provide valuable insight into the effects of natural and anthropogenic disturbances, and allow scientists and forest managers to determine which management regimes succeed and which ones fail in terms of desired objectives. Unfortunately, many long-term studies are closed before the full benefits of the research can be realized. U.S. Forest Service experimental forests represent a large portion of long-term research in the United States.

The Paul Smith, Finch-Pryun, and Gale River Experimental Forests (EFs) were all established in the early to mid 1900s. Each of these was closed after silvicultural experiments were initiated; those studies could have provided essential information to land managers and researchers today. At the time, however, changing societal needs and research priorities led to redirected staffing and funding, and all three EFs were disestablished. As a consequence, initial investments in the EFs were lost and the outcomes of the experiments were not fully realized.

This is a partial annotated bibliography containing examples of the publications from the three historical experimental forests. While all publications are not included, the publications found in this appendix are primary publications which cover a full range of studies conducted in early northern mixed-conifer forests.

Adirondack Research Center: Paul Smith and Finch-Pruyn Experimental Forests

Curry, J.R. and Church, T.W. 1952. Observations on winter drying of conifers in the Adirondacks. Journal of Forestry. 50(2): 114-116.

This article discusses the cause and effect of conifer needle browning and defoliation during the winter months in the Adirondack Mountains of New York, including at the Paul Smith EF. Needle browning was observed after periods of severe cold followed by warming weather with high winds. Red spruce was the most heavily affected species, followed by balsam fir, eastern hemlock and white pine.

Curry, J.R. and Rushmore, F.M. 1955. Experiments in killing northern hardwoods with sodium arsenite and ammonium sulfamate. Journal of Forestry. 53(8): 575-580.[3]

Experiments involving the use of sodium arsenite and ammonium sulfamate for killing hardwoods were employed in the Adirondack Mountains of New York. It was found that treatments in the summer months using sodium arsenite were the most effective.

Recknagel, A.B. 1933. Sustained yield of Adirondack spruce and fir. Journal of Forestry. 33 (3): 343-344.

[3] The experiments reported in this paper are believed to be conducted on the PSEF or FPEF.

This article describes the diameter limits used for the plots on the Finch-Pruyn EF. In order to achieve the greatest amount of return, it was suggested that spruce should be cut to 10" dbh and fir should be cut to 6" dbh. This was believed to enable the forest to be continually productive while maintaining the wood capital.

Recknagel, A.B., H.L. Churchill, C. Heimberger, and M. Westveld. 1933. Experimental cutting of spruce and fir in the Adirondacks. Journal of Forestry 31(6): 680-688.

Plots were established on the Finch-Pruyn Experimental Forest near Newcomb, NY in order to determine ideal cutting cycles for pulp-producing lands. Plots were harvested at varying intensities and measured to determine amounts and types of reproduction as well as the amount of slash remaining. This experiment was intended to be a long-term monitoring project.

Recknagel, A.B. and Westveld, M. 1942. Results of second remeasurement of Airondack cutting plots. Journal of Forestry. 40 (11): 837-840.

This article describes the five, 28-acre cutting and girdling plots established on the Finch-Pruyn EF. It was determined that insufficient time had passed to fully understand what degree of cutting cycle is optimum for commercial requirements for spruce and fir. Logging may reduce advance conifer reproduction and hardwoods left standing may impede the development of understory softwoods.

Rushmore, F.M. 1956a. The frill: a new technique in chemical debarking. Journal of Forestry. 54 (5): 329-331.

Simple frilling consists of axe cuts made around the circumference of a tree bole which are then treated with sodium arsenite. This method, which was applied on the Paul Smith EF, was easier, cheaper than and just as effective as previous methods used including complete girdling.

Rushmore, F.M. 1956b. A small quantity of sodium arsenite will kill large cull hardwoods. Sta. Pap. 83. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 6 p.[4]

This article demonstrates that large quantities of sodium arsenite may not be required when killing large, cull hardwoods. Unlike previous studies using up to 32 cc of the chemical, this study found that doses as low as 2 cc at 8-inch intervals would kill large trees within 3 years.

Rushmore, F.M. 1957. The Adirondack Research Center. Sta. Pap. NE-98. Upper Darby, PA. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station.18 p.

[4] This station paper is from the Paul Smith Experimental Forest.

This article is a historical overview of the Adirondack Research Center located in Paul Smiths, NY. It discusses the goals of the research center as well as the details regarding the Finch-Pruyn Experimental Forest and Paul Smith Experimental Forest.

Rushmore, F.M. 1958. Sodium arsenite in spaced ax cuts: an effective stand-improvement technique. Journal of Forestry. 56 (3): 195-199.

This article describes the history of chemical use in killing hardwoods and the use of chemicals at the Finch-Pruyn EF. Axes were used with different spacing prior to applying the chemicals. This was determined an effective method of killing unwanted trees.

Westveld, M. 1933. Experimental cutting area in the Adirondacks. Journal of Forestry. 31 (5): 599.

This article describes the Finch-Pruyn Experimental Forest near Newcomb, NY. The experimental area cover approximately 150 acres divided into 5 nearly equal sized plots. Different diameter-limit cuttings were applied to spruce and fir with some degree of girdling to increase growth of residual softwoods.

Gale River Experimental Forest

Belotelkin, K.T., Reineke, R.H., Westveld, M. 1942. Spruce-fire selective logging costs. Journal of Forestry: 326-336.

This article examines the feasibility of partial cutting as opposed to clearcutting. Previous assumptions have led to the widespread belief that clearcutting is cheaper, however, this is not necessarily the case. A partial cutting experiment on the Gale River Experimental Forest found that costs of clearcutting and partial cutting were essentially equal.

Kraemer, J.H. 1937. Suggestions for silvicultural measures in old field spruce-fir stands in the Northeast. Journal of Forestry. 35 (10): 948-953.[5]

This article details the importance of maintaining timber productivity of old field spruce – fir stands in the Northeast. The author suggests that the only way that this is possible to replace clearcutting practices with partial cutting practices. This method would not only reduce the amount of slash on the ground, it would also ensure advance reproduction of spruce and fir.

Westveld, M. 1938. Silvicultural treatment of spruce stands in northeastern United States. Journal of Forestry. 36: 944-950.

Silvicultural treatments in the Northeast should focus on ensuring adequate spruce and fir reproduction prior to harvesting and to reduce pressures from hardwood competition after harvesting. Westveld suggested that partial cutting is ideal because it allows inferior trees

[5] Although not stated directly, this article discusses permanent plots in New Hampshire which may be part of the Gale River Experimental Forest.

to be removed while increasing spruce sawlog production. This paper includes a description of the partial cutting experiment on the Gale River EF, as well as a general description of weeding.

Westveld, M. 1951. Vegetation mapping as a guide to better silviculture. Ecology. 32(3): 508-517.

This article stresses the importance of assessing natural ecological patterns when making silvicultural decisions. In the northeast, this is difficult due to harvesting history; however two ways in which this may be accomplished are 1) interpreting existing cover types and 2) using indicator plants to deduce what forest types are adapted to the site. The relationship between forest type and ground vegetation type on the Gale River EF is examined.

Additional Papers

Berven, K.A., Kenefic, L.S., Weiskittel, A.R., Wilson, J., Twery, M. In press. In: Long Term Forest Research. Irland, L.C. and Camp, A.E., eds. The lost research of early northeastern spruce – fir experimental forests: A tale of lost opportunities.

This paper addresses three early spruce – fir experimental forests. They include the Paul Smith EF, the Finch-Pruyn EF and the Gale River EF. These experimental forests were monumental in advocating uneven-aged silviculture in the northern mixed-conifer forest type. These forests were closed primarily due to a loss of scientific relevance, however natural disaster contributed. Paperwork from the experiments was lost over time so study continuation was deemed impossible. Retaining ownership of files is key to future use.

APPENDIX B: FVS-NE MODELING SCENARIO

Long-term forest datasets provide opportunities to test model strengths and weaknesses. FVS-NE (Forest Vegetation Simulator-Northeast Variant) is an empirical, single-tree, distant-independent model designed by the U.S. Forest Service. The range of the model is extensive, covering 13 states from Ohio to Maine. The spatially extensive nature of this model is complicated by diverse array of forest types throughout the region.

The Penobscot EF is an exemplary illustration of replicated, long-term research. Because of this, a modeling case study was conducted using the Forest Vegetation Simulator - Northeast Variant (FVS-NE) and FVS-NE (Beta). The modeling was conducted in 6 compartments over 3 treatments. Long-term modeling was conducted post treatment for commercial clearcutting (compartments 8 and 22, also called unregulated harvesting) and 3-stage shelterwood treatments (compartments 23B and 29B) and from the unmanaged reference (compartments 32A and 32B). Results comparing predicted and observed basal area for FVS-NE and FVS-NE (Beta) are found in tables B.1 and B.2. Where years overlap between PEF inventory and FVS projections, residuals were plotted against inventory years (Figures B.1 and B.2). Because there was only the initial overlapping year in the 3-stage shelterwood, it was removed from the residual analysis.

Results show that FVS-NE and FVS-NE (Beta) slightly overestimated basal area in all compartments except for the 3-stage shelterwood (C23B and C29B), which was highly underestimated. This indicates that FVS may not be appropriate for certain silvicultural treatments. Residuals exhibit greater ranges around zero as time progresses. There was not a significant difference between FVS-NE and FVS-NE (Beta).

Table B.1. Actual and FVS-NE predicted basal area per acre for three treatments on the Penobscot Experimental Forest.

	Actual 22	FVS 22	Actual 8	FVS 8	Actual 23B	FVS 23B	Actual 29B	FVS 29B	Actual 32A	FVS 32A	Actual 32B	FVS 32B
1954									148.78	148.67	155.24	155.0
1959										170.17		168.67
1960									139.32		156.13	
1964										186.83		179.67
1965									129.50		160.65	
1969										197.67		188.33
1970									120.95		171.01	
1972					4.00	3.84						
1974								3.11		205.50		196.33
1975					5.84		3.60		115.87		178.68	
1977						20.77	5.55					
1979								10.78		211.0		203.0
1980					29.53				116.87		187.54	
1982						42.15	13.62					
1983			14.89									
1984								21.44	115.50	216.17	191.75	210.0
1985							21.81					
1987			17.32	21.81		61.85						
1989	23.73							31.44	127.93	220.33	202.14	214.67
1990					133.55							
1991							67.97					
1992	31.46	40.93	37.75	63.85		79.77						
1993									135.04	223.83	215.19	
1994								41.22				218.33
1995					170.81							
1997		66.80		106.05		95.08	105.47					
1998	55.05		65.79									
1999								50.44	152.90	226.50	216.18	221.0
2001					196.65		132.68					
2002		92.60		133.86		108.85						
2004	91.46							58.89		228.67		224.0
2007		112.67		151.90		121.23						
2008			119.97									
2009								66.11	177.35	230.67	222.35	226.33
2010					247.63		162.45					
2011												
2012		128.06		165.57		131.15						
2013												
2014										232.16		228.67

Table B.2. Actual and FVS-NE (Beta) predicted basal area per acre for three treatments on the Penobscot Experimental Forest.

	Actual 22	FVS 22	Actual 8	FVS 8	Actual 23B	FVS 23B	Actual 29B	FVS 29B	Actual 32A	FVS 32A	Actual 32B	FVS 32B
1954									148.78	150.78	155.24	155.0
1959										185.67		178.67
1960									139.32		156.13	
1964										201.56		193.67
1965									129.50		160.65	
1969										213.33		207.67
1970									120.95		171.01	
1972					4.00	3.84						
1974								3.11		220.78		215.0
1975					5.84		3.60		115.87		178.68	
1977						16.84	5.55					
1979								11.67		226.11		220.0
1980					29.53				116.87		187.54	
1982						39.15	13.62					
1983			14.89									
1984								25.89	115.50	229.33	191.75	225.0
1985							21.81					
1987			17.32	21.80		66.08						
1989	23.73							38.22	127.93	230.67	202.14	229.0
1990					133.55							
1991							67.97					
1992	31.46	40.93	37.75	75.19		85.0						
1993									135.04	231.33	215.19	
1994								46.56				231.33
1995					170.81							
1997		70.07		128.57		97.92	105.47					
1998	55.05		65.79									
1999								52.89	152.90	231.78	216.18	232.33
2001					196.65		132.68					
2002		104.53		161.62		110.85						
2004	91.46							59.44		232.0		233.0
2007		130.47		176.81		121.69						
2008			119.97									
2009								65.78	177.35	232.11	222.35	233.33
2010					247.63		162.45					
2011												
2012		151.60		187.14		132.15						
2013												
2014										232.56		234.0

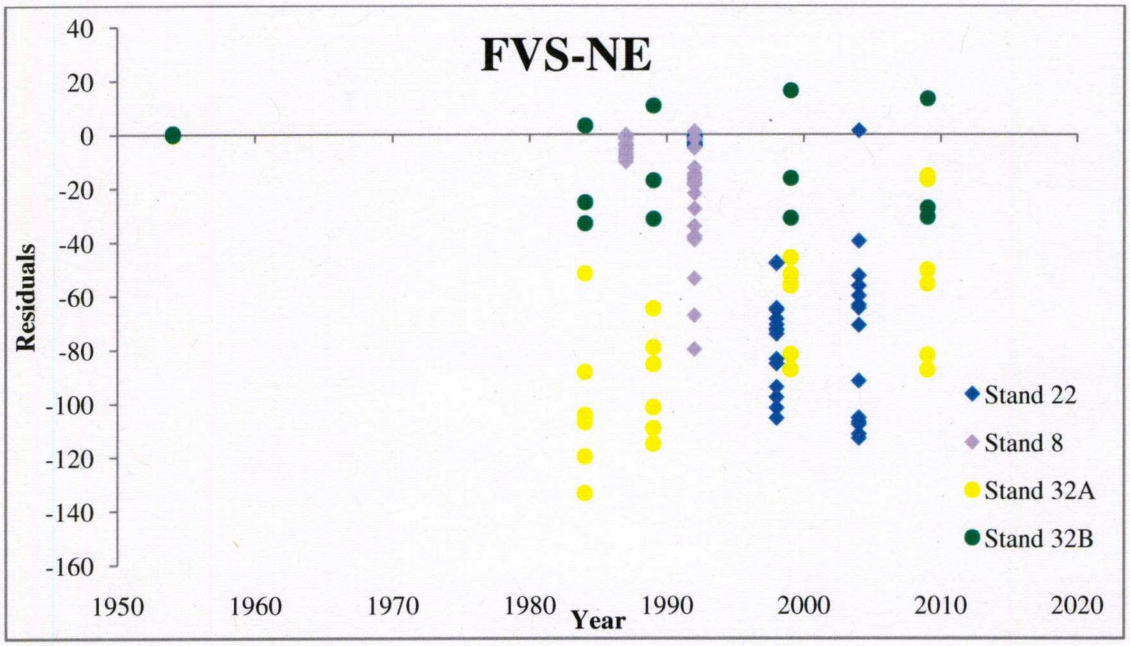

Figure B.1. Plot-level residuals (observed – predicted) of predicted stand basal area (ft^2 ac^{-1}) by compartment using FVS-NE on the Penobscot Experimental Forest.

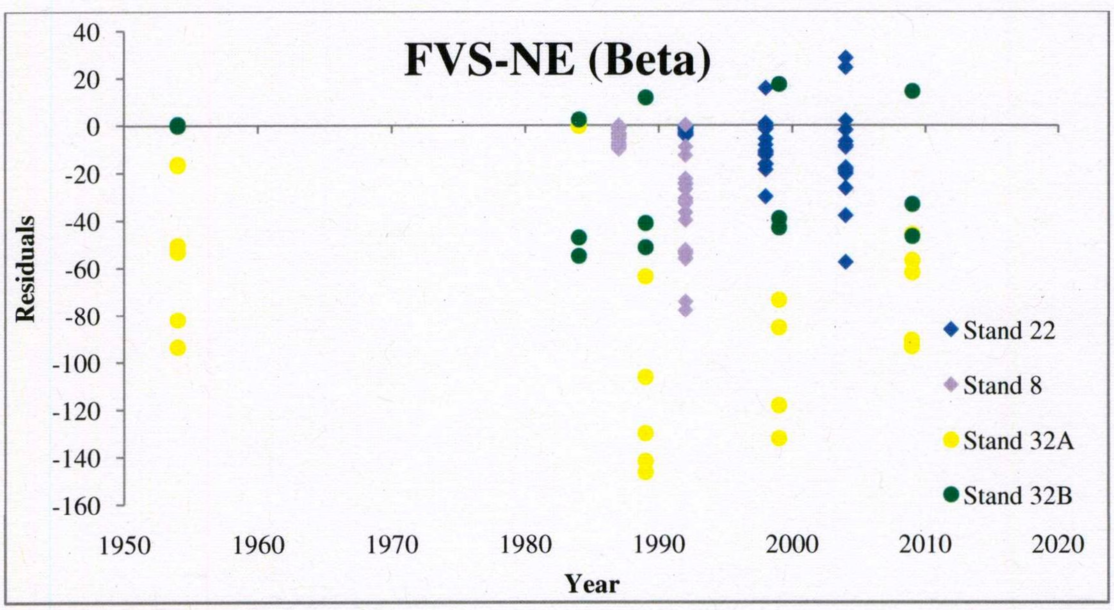

Figure B.2. Plot-level residuals (observed – predicted) of predicted stand basal area (ft^2 ac^{-1}) by compartment using FVS-NE (Beta) on the Penobscot Experimental Forest.

BIOGRAPHY OF THE AUTHOR

Kate Berven was born on August 13, 1978. Kate went to the University of Tennessee in Knoxville, TN, after serving almost nine years in the United States Navy. Initially a Biology major, she wanted a career which would be more “hands-on” in conservation and forest stewardship. Kate majored in Forestry and graduated magna cum laude in May of 2009.

While at the University of Tennessee, Kate worked for Tennessee’s Division of Forestry as an intern in Forest Inventory Analysis (FIA). She also volunteered at the raptor rehabilitation center in Clinton, Tennessee caring for injured and educational birds of prey. Knowing that she wanted to continue her education and learn about forestry in a different region, Kate applied to graduate school at the University of Maine in Orono, Maine.

Kate lives in Holden, Maine with her husband Ryan and stepson Nathan. She is a candidate for the Master of Science degree in Forest Resources at the University of Maine in August, 2011.